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À Abbie, Eva et Thea

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AVANT-PROPOS

Cette thèse comporte trois chapitres rédigés sous forme d'articles. À titre de candidat à au doctorat, j'ai procédé à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Le premier article "Are old boreal forests a safe bet for the conservation of the avifauna associated with decayed wood in eastern Canada?" a été publié dans la revue *Forest Ecology and Management* en 2017 (385: 127-139). Le deuxième article "Persistence, changes, and robustness in ecological networks at the transition between mixedwood and coniferous boreal forests: the case of nest webs" sera soumis sous peu dans la revue *Ecology*. Le troisième article "The Pileated Woodpecker (*Dryocopus pileatus*): an umbrella species for cavity nesters in boreal forests" sera soumis sous peu dans la revue *Biological Conservation*. En tant que directeur de thèse, Pierre Drapeau est coauteur des trois articles. De plus, Alexandre Fouillet est coauteur du deuxième chapitre, car il a participé à l'élaboration du protocole de recherche et à la récolte de données sur le terrain et à la conception de l'article. Le troisième chapitre découle d'un stage doctoral avec Antoine Nappi du Bureau du forestier en chef du Québec et avec Marianne Cheveau du Ministère des Forêts, de la Faune et des Parcs du Québec. Ces deux chercheurs ont participé à l'élaboration et à la direction du projet et ils s'ajoutent à cette étude comme coauteurs. De plus, Alain Leduc a participé à l'élaboration du projet et aux analyses statistiques et est ajouté comme coauteur de ce chapitre.

Cette thèse a été défendue le 6 octobre 2016 à l'Université du Québec à Montréal. Les membres du jury de thèse étaient :

Pierre Drapeau, professeur, directeur de thèse, Département des sciences biologiques, Université du Québec à Montréal;

Daniel Kneeshaw, professeur, président du jury, Département des sciences biologiques, Université du Québec à Montréal;

Louis Imbeau, professeur, Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue;

Jean-Michel Roberge, professeur associé, Department of Wildlife, Fish and Environmental Studies, Université suédoise des sciences agricoles.

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RÉSUMÉ

Les vieilles forêts constituent des habitats clés pour la diversité biologique en forêt boréale. Elles sont cruciales au maintien des espèces qui utilisent les arbres à cavités dans nos paysages forestiers, grâce entre autres, à un apport substantiel et constant d'arbres sénescents et morts. Toutefois, un important gradient latitudinal passant de la forêt mixte à la forêt de conifères démarque la forêt boréale de l'est du Canada. Ce gradient de composition du couvert forestier se traduit par une réduction considérable de la disponibilité d'arbres morts et sénescents de grand diamètre, et donc de la qualité des substrats de nidification et d'alimentation de la faune utilisatrice d'arbres à cavités. L'abondance et la qualité réduites de ces ressources comptent parmi les causes probables de la limite nordique de répartition de plusieurs espèces de ce groupe. La réponse fonctionnelle de la faune cavicole à ces changements régionaux de composition et de structure du couvert forestier boréal demeure peu connue. Cette thèse propose une analyse quantitative de cette question selon des thèmes qui abordent dans trois chapitres ; (1) la distribution de la faune associée aux arbres à cavités en région de pessière à mousses (2), la structure des réseaux d'utilisateurs de cavités entre les régions de la forêt mixte et de la forêt de conifères dominées par l'épinette noire et enfin (3) le rôle d'espèce parapluie du Grand Pic (*Dryocopus pileatus*).

Le premier chapitre examine l'importance des forêts âgées mixtes et de conifères pour les oiseaux associés au bois sénescent et mort selon un gradient d'âge, de structure et de composition forestière en pessière à mousses, une portion de la forêt boréale dominée par une matrice d'épinettes noires. Nos résultats montrent que les vieilles forêts mixtes qui ne représentent que 4 % du recouvrement forestier dans cette région d'étude étaient de loin les plus utilisées par l'avifaune associée au bois sénescent et mort. Dans les vieilles forêts de conifères, ces oiseaux ont montré une réponse modale au vieillissement alors que leur richesse en espèces atteint son maximum à 160 ans pour décliner par la suite. Les très vieilles forêts entourbées, représentant plus de 40 % du territoire d'étude, ont étés associées à une richesse d'espèces significativement plus pauvre d'oiseaux cavicoles et corticoles. La diversité structurale des tiges est la variable d'habitat qui explique le mieux la richesse d'espèces de ce groupe fonctionnel ainsi que l'abondance de traces d'alimentation des pics. Chez les espèces individuelles, la quantité et la qualité d'arbres morts dans un peuplement expliquent le mieux leur occurrence et l'abondance de leurs traces d'alimentation. Nous concluons qu'en pessière à mousses la conservation de l'avifaune associée au bois mort devrait être priorisée dans les peuplements productifs mixtes et résineux.

Le deuxième chapitre traite du changement, de la persistance et de la robustesse des réseaux écologiques le long d'un gradient latitudinal traduisant la transition de la composition d'un couvert forestier dominé par des peuplements mixtes à un couvert dominé par les conifères, qui s'étend sur plus de 200 km en forêt boréale. Les réseaux d'utilisateurs de cavités dans ce biome sont souvent composés d'une minorité d'espèces ayant de nombreuses interactions. Il est suggéré que de tels réseaux soient peu robustes à la perte d'espèces clés de voûte. De plus, tout au long de ce gradient un agent important de transformation des habitats forestiers, le castor d'Amérique (*Castor canadensis*) inonde par ses ouvrages de rétention d'eau des forêts qui entraînent la mortalité synchrone d'arbres qui deviennent propices à être excavés par les pics et utilisés par la communauté cavicole. À l'aide de données portant sur la reproduction d'espèces cavicoles récoltées le long de ce gradient latitudinal, tant dans les forêts fermées que dans les forêts ouvertes inondées par le castor nous montrons que des changements structurels dans les réseaux d'utilisateurs de cavités sont associés à des changements importants dans la disponibilité d'arbres adéquats à l'excavation de cavités. Nous observons que le rôle clé joué par le peuplier faux-tremble persiste dans les forêts mixtes au nord de ce gradient qui sont souvent isolées et ne représentent qu'une très faible proportion du territoire dans ces grandes matrices forestières résineuses. Ces forêts ont des réseaux riches, complexes et très similaires à ceux trouvés dans les forêts mixtes situées plus au sud. Au contraire, les forêts boréales résineuses avaient une densité très faible d'arbres de nidification. Nous montrons que les peuplements forestiers inondés par le castor ont hébergé des réseaux riches et complexes dans les deux régions. Tandis que le Grand Pic reste tant au nord qu'au sud de la forêt boréale, l'espèce clé de voûte pour les utilisateurs secondaires de grande taille en forêts fermées, le Pic flamboyant, était l'espèce responsable de la majorité de cavités de moyenne à grande taille dans les forêts résineuses à canopée ouverte et fermée. Des analyses simulant le retrait d'espèces clés de voûte montrent que les réseaux des forêts fermées sont peu robustes à la perte du peuplier faux-tremble et à moindre degré, à la perte du Grand Pic. Les forêts inondées par le castor montrent une plus grande robustesse due à une diversité accrue d'espèces d'arbres pour l'excavation de cavités.

Ayant ciblé dans les chapitres précédents les vieilles forêts mixtes de peuplier faux-tremble comme des habitats à prioriser pour la conservation de l'avifaune associée au bois mort et le Grand Pic comme une espèce clé de voûte, le troisième chapitre porte sur l'évaluation de cet excavateur comme une espèce parapluie pour la faune cavicole en forêt boréale. Nous vérifions l'hypothèse selon laquelle la conservation de l'habitat pour le Grand Pic conserverait aussi l'habitat des autres espèces cavicoles vu que cette espèce est très exigeante en ce qui concerne la qualité de son habitat. Nos résultats montrent que le Grand Pic sélectionne fortement les peuplements qui sont aussi sélectionnés par la grande majorité des utilisateurs de cavités : les vieux peuplements de forêts mixtes avec peupliers faux-trembles. Le Grand Pic est l'espèce dont la présence d'une cavité à un site est la plus susceptible de prévoir la présence de

cavités de nidification des autres espèces cavicoles. De plus, son modèle de sélection d'habitats est celui qui explique le mieux la richesse des autres espèces cavicoles et qui s'avère être le plus efficace pour prioriser les sites les plus riches en espèces cavicoles. Le Grand Pic peut donc être considéré comme une espèce parapluie pour ce qui est de la qualité de l'habitat de reproduction de l'ensemble de la faune cavicole associée aux forêts mixtes, un compartiment clé de la biodiversité en forêt boréale.

Cette thèse montre que l'âge, la productivité et la composition des forêts boréales sont des facteurs clés dans le maintien de la diversité spécifique et fonctionnelle de la faune associée au bois sénescent et mort. Les vieilles forêts mixtes, malgré leur faible représentation dans le paysage sont désignées comme habitats clés et devraient être ciblées pour la conservation. Dans ces forêts, le Grand Pic joue le double rôle d'espèce clé de voûte et d'espèce parapluie pour la faune cavicole. Les vieilles forêts résineuses sont généralement pauvres, mais semblent cruciales pour l'alimentation du Pic à dos noir et du Pic à dos rayé. Toutefois, la faible contribution des vieilles forêts résineuses aux réseaux d'utilisateurs de cavités est compensée par les réseaux complexes d'espèces cavicoles dans les forêts ouvertes par l'activité du castor dans les marais sur l'ensemble du territoire.

Mots-clés : forêt boréale, bois sénescent et mort, pics, faune cavicole, sélection d'habitat, réseaux d'utilisateurs de cavités, paludification, robustesse, peuplier faux-tremble, épinette noire

ABSTRACT

Old-growth forests are key habitats for the biodiversity in the boreal forest. They are crucial to the maintenance of species that use cavity trees in our forest landscapes, partly because they provide a substantial and constant amount of senescent and dead trees. However, there is an important latitudinal gradient in the boreal forest, going from mixedwood forests to coniferous forest in eastern Canada. In this gradient of forest cover composition there is a considerable reduction in the availability of large diameter senescent and dead trees, and thus of trees adequate for nesting and foraging for the dead wood associated fauna. The low availability or quality of these resources is the probable cause of the northern distribution limit for many of these species. The functional response of cavity nesters to these regional changes in composition and structure of boreal forest cover remains mostly unknown. This thesis proposes a quantitative analysis of this question while addressing the following themes: (1) the distribution of the fauna associated with cavity trees in the black spruce moss region (2), the network structure of cavity users between the mixedwood regions and the black spruce feather moss region and finally (3) the umbrella species role played by the Pileated Woodpecker (*Dryocopus pileatus*).

The first chapter examines the importance of old mixed and coniferous boreal forests for decaying and dead wood associated birds along a forest age, structure and composition gradient in black spruce feather moss, a portion of the boreal forest dominated by black spruce stands. The results show that even though old mixedwood stands represent only 4 % of the forest cover in the study region, these forests were by far the most used by the deadwood avifauna. In old coniferous stands, these birds had a modal response to forest age with species richness reaching their peak at 160 years followed by a decline. Representing more than 40 % of the landscape, old paludified stands were associated with a significantly lower species richness of deadwood birds. Structural diversity was the habitat variable that best explained species richness and abundance of woodpecker foraging marks on trees. At the level of individual species the quantity and quality of dead trees in the stand best explained the species occurrence and abundance of foraging marks. We conclude that in the black spruce feather moss, productive coniferous and mixedwood stands should be prioritized for the conservation of the deadwood associated avifauna.

The second chapter investigates the changes, the persistence and the robustness of ecological networks along a latitudinal gradient in the boreal forest, going from mixedwood to coniferous dominated forest cover stretching for more than 200 km in the boreal forest. Nest webs in this biome are often composed of a few highly connected species suggesting low robustness to the loss of keystone species. In addition, along this gradient an important agent of transformation of forested habitat,

the American beaver (*Castor canadensis*) flood forests by retaining water and causes synchronous tree mortality that becomes propitious to cavity excavation by woodpeckers and use by the cavity-nesting community. With data on the reproduction of cavity nesters collected along this latitudinal gradient, as much in closed forest than in open forest flooded by the beaver we show that structural changes in nest webs are associated to drastic changes in the availability of trees adequate for cavity excavation. We observed that the key role played by the trembling aspen persists in mixedwood forests in the northern portion of this gradient, which are often isolated and represent only a small portion of the territory dominated by coniferous forests. These forests had rich and complex networks very similar to those found in southern mixedwoods. To the contrary, coniferous forests had very low nest tree densities. We demonstrate that forests flooded by the actions of the beaver harbored similarly rich and complex nest webs in both forest regions. Whereas the Pileated Woodpecker (*Dryocopus pileatus*) remained the pivotal species for large secondary cavity users in closed-canopy forests dominated by trembling aspen in both forest regions, the Northern Flicker was the main provider of medium to large cavities in open forests and in closed-canopy black spruce stands. Targeted removal simulations highlighted that closed-canopy forest networks had low robustness to the removal of trembling aspen and to a lesser degree to the loss of the Pileated Woodpecker. The majority of links within these networks were driven by these two species. Open forests created by beaver ponds showed more robust nest webs mainly because primary excavators relied on a higher diversity of tree species, downsizing the use of trembling aspen.

Having identified in chapters one and two old mixedwoods with trembling aspen as key habitats and the Pileated Woodpecker as a keystone species, the third chapters aimed to evaluate this large cavity excavator as an umbrella species for cavity nesters in the boreal forest. We verify the hypothesis that the conservation of the Pileated Woodpecker's habitat would also conserve the habitat for other cavity nesters since this species is very demanding in terms of habitat quality. Our results show that the Pileated Woodpecker strongly selects forest stands also selected by the majority of cavity nesters: old mixedwoods with trembling aspen. The Pileated Woodpecker is the species in which the presence of its cavities at a site was the most susceptible to predict the presence of other species nesting cavities. With a simulation of site selection for conservation of cavity nesters, we show that prioritizing sites with the Pileated Woodpecker as an umbrella species is efficient. Hence, the Pileated Woodpecker is depicted as an umbrella species for the quality of reproduction habitat for cavity nesters associated with mixedwoods, a key component of biodiversity in boreal forests.

This thesis demonstrates that age, productivity and composition of boreal forests are key factors for maintaining specific and functional diversity of decayed and dead wood associated fauna. Despite their low availability in the landscape, old

mixedwood forests are key habitats and are targeted as habitats of special concern for conservation. In these forests, the Pileated Woodpecker plays the double role of keystone and umbrella species for the cavity nesters. Old coniferous forests are generally poor but seemed crucial for the foraging of the Black-backed Woodpecker and the American Three-toed Woodpecker. However, even in the absence of these old forests, complex cavity users networks composed of open canopy forest associated species persisted in beaver ponds throughout the latitudinal gradient.

Keywords: boreal forest, senescent and dead wood, woodpeckers, cavity nesters, nest webs, paludification, robustness, Pileated Woodpecker, trembling aspen, black spruce

INTRODUCTION GÉNÉRALE

Importance du bois mort pour la biodiversité

La dégradation et la décomposition des arbres sont responsables de la présence d'une grande diversité d'organismes dans nos forêts : champignons, insectes, oiseaux et mammifères (Franklin et al. 1987, Siitonen 2001). La mort des arbres en particulier offre une ressource clé pour l'alimentation et la reproduction de multiples espèces (Thomas 1979, Harmon et al. 1986, Franklin et al. 1987, Darveau et Desrochers 2001, Bunnell et al. 2002, Grove 2002, Nappi et al. 2015). Pour certains groupes d'espèces, une stratégie évolutive efficace combine le site d'alimentation et le site de reproduction sur le bois mort; à titre d'exemple, les insectes saproxiliques se reproduisent et leurs larves se nourrissent et creusent des tunnels dans le bois mort. En revanche, certains pics se nourrissent de ces insectes et excavent leurs cavités de reproduction dans des arbres morts et sénescents. Le bois sénescent et mort est donc à la base de réseaux écologiques complexes. Depuis une trentaine d'années, la communauté scientifique accorde une importance de plus en plus grande au bois mort pour le maintien de la biodiversité dans nos forêts (Thomas 1979, Harmon et al. 1986, Grove 2002, Stockland et Siitonen 2012). En forêt boréale Fenno-scandinave, où l'on a considérablement réduit la disponibilité du bois mort, plusieurs espèces dépendantes de cette ressource sont menacées ou localement éteintes (Angelstam et Mikusiński 1994, Siitonen 2001). Parmi les espèces fauniques associées au bois mort, les pics constituent un groupe facilement mesurable qui pourrait être utilisé comme groupe d'espèces indicatrices de l'état de la diversité biologique (Angelstam et Mikusiński 1994, Mikusiński et al. 2001, Virkkala 2006, Drever et al. 2008). Les espèces d'oiseaux résidentes qui dépendent des cavités dans les arbres morts ou

sénescents seraient hautement vulnérables à la diminution de la disponibilité du bois mort causée par l'aménagement forestier (Imbeau et al. 2001).

La dynamique du recrutement de bois mort en forêt boréale

En forêt boréale, comme dans toutes les forêts sous l'influence d'un régime de perturbations naturelles, la répartition des arbres morts ou sénescents dans les peuplements et dans le paysage est hétérogène (Franklin et al. 1987). Le feu est reconnu comme étant la perturbation naturelle la plus importante influençant la distribution des classes d'âge et la composition du couvert forestier (Rowe et Scotter 1973, Bergeron et al. 2001, Bergeron et al. 2004, Gauthier et al. 2008b). Cette perturbation majeure génère un recrutement massif d'arbres récemment morts qui sont rapidement colonisés par les insectes xylophages (Saint-Germain et al. 2004c, Saint-Germain et al. 2004b, Saint-Germain et al. 2004a). Parmi les espèces de vertébrés associées au bois mort, le Pic à dos noir (*Picoides arcticus*) compte parmi les espèces les plus associées à ces importants, mais éphémères, apports de ressources alimentaires (Hutto 1995, Imbeau et al. 1999, Nappi 2009). Les brûlis récents sont considérés comme des habitats sources pour le Pic à dos noir, offrant à la fois des conditions de nidification et d'alimentation un substrat d'alimentation adéquat pour ceux-ci (Hutto 1995, Murphy et Lehnhausen 1998, Nappi 2009, Nappi et al. 2010, Nappi et Drapeau 2011). En l'absence de perturbations primaires telles que le feu, des perturbations naturelles secondaires peuvent réguler la composition et la structure forestière (Kneeshaw et Bergeron 1998). Les épidémies d'insectes, dont celles de la tordeuse de bourgeons d'épinette, ont d'importants effets sur la structure forestière ; elles créent des trouées et participent à l'apport en bois mort utilisé par la faune (Goggans et al. 1989, Kneeshaw et Bergeron 1998, Morin et al. 2008, Bonnot et al. 2009). En revanche, la sénescence des arbres combinés à d'autres facteurs biotiques et abiotiques (vent, maladies, infection fongique) est responsable d'un recrutement

constant d'arbres morts de grand diamètre dans les paysages boréaux (Franklin et al. 1987).

Le rôle du castor (*Castor canadensis*) comme un agent de perturbation en forêt boréale est souvent négligé par la littérature puisque des perturbations à plus grande échelle sont priorisées (Nummi et Kuuluvainen 2013). Par contre, considéré par plusieurs comme une espèce-ingénieur, le castor est responsable de l'ennoiement et la mort d'une quantité non négligeable d'arbres et de la création de marécages et de terres humides, et par ce fait, de la création d'habitats pour une variété impressionnante d'espèces (Jones et al. 1994, Wright et al. 2002, Rosell et al. 2005, Nummi et Kuuluvainen 2013). Il est proposé que cette espèce-ingénieur augmente la richesse d'espèces à l'échelle du paysage (Wright et al. 2002). En l'absence de perturbations majeures et dans des paysages dominés par des épinettes noires de petite taille, les forêts ennoyées par le castor sont possiblement une source importante d'arbres adéquats à l'excavation de cavités. À date, très peu d'études ont abordé la question de l'utilisation par les pics des forêts inondées par le castor (Lochmiller 1979, Grover et Baldassarre 1995) et nous n'avons répertorié aucune étude publiée avec révision par des pairs ayant vérifié l'importance de cet habitat pour l'ensemble de la communauté d'utilisateurs de cavités.

Les forêts qui ont échappé aux feux et autres perturbations suivent une trajectoire successionnelle qui diffère selon leur composition (Bergeron 2000, Harvey et al. 2002). En pessière noire à mousses, où l'on retrouve une majorité de peuplements purs d'épinettes noires (*Picea mariana*), ce sont principalement des changements dans la structure forestière qui s'effectuent à mesure que les forêts vieillissent, ces forêts devenant graduellement plus structurellement complexes (Harper et al. 2002, Harper et al. 2005). Des changements considérables dans la structure et la composition forestière se produisent tout au long du vieillissement des forêts boréales mixtes débutant par le peuplier faux-tremble (*Populus tremuloides*). Pour la portion

sud de la forêt boréale mixte, ces forêts passent d'une dominance feuillue et d'une structure homogène à une forêt dont la canopée est mixte et finalement à une forêt qui est dominée par les conifères dont la structure est plus hétérogène (Harvey et al. 2002). Dans la portion nord de la forêt boréale, la succession forestière peut commencer par le peuplier faux-tremble, le pin gris ou l'épinette noire, mais converge dans le temps autour de peuplements d'épinettes noires (Bergeron et al. 2002, Harper et al. 2003).

Le long d'un gradient successionnel, l'apport maximal d'arbres morts et sénescents est généralement atteint à la sénescence des peuplements, lorsque les arbres de la première cohorte meurent de vieillesse et se font graduellement remplacer par les arbres de la seconde cohorte (Clark et al. 1998, Franklin et al. 2002, Kneeshaw et Gauthier 2003, Harper et al. 2005). Kneeshaw et Gauthier (2003) définissent ces forêts comme étant des forêts anciennes (old-growth forests). Le recrutement de bois mort par la sénescence s'échelonne sous une plus longue période de temps. De ce fait, plusieurs espèces d'oiseaux associées au bois mort sont aussi associées aux forêts âgées ou anciennes (Angelstam et Mikusiński 1994, Drapeau et al. 2000, Schieck et Song 2006). Entre autres, la plupart des excavateurs de cavités en forêt boréale sont associés aux vieilles forêts (Imbeau 2001, Drapeau et al. 2003, Savignac et Machtans 2006, Cooke 2009, Cadieux 2011). Ces vieilles forêts boréales sont largement distribuées dans le territoire et assurent un apport constant d'arbres morts pour une panoplie d'états de dégradation aux espèces qui en dépendent.

Cela dit, l'apport continu en bois mort n'est pas une fonction partagée par toutes les vieilles forêts. Dans les basses terres de la baie James, dans la ceinture d'argile du Québec et de l'Ontario, où la topographie est plate et non accidentée (Robitaille et Saucier 1998), les vieilles forêts d'épinettes noires en pessière à mousses ont tendance à s'entourber à mesure qu'elles vieillissent (Fenton et al. 2005). L'accumulation de matière organique au sol, principalement de sphaignes de lumière,

cause la baisse de la température du sol et de la disponibilité en nutriments. Cet entourbement, aussi appelé paludification, cause une diminution importante de la productivité forestière (Simard et al. 2007) et, par conséquent, du recrutement de gros arbres et de bois mort (Harper et al. 2005).

L'utilisation des arbres morts par la faune cavicole et corticole en forêt boréale

En forêt boréale sous l'influence d'un régime de perturbations naturelles, il y a généralement un apport constant d'arbres morts et sénescents. Plusieurs espèces d'oiseaux forestiers se sont adaptées au cours de leur évolution à l'utilisation de cette ressource pour subvenir à leurs besoins vitaux : l'alimentation, la nidification, les refuges et la communication acoustique (Darveau et Desrochers 2001).

Une partie importante de la faune vertébrée des forêts boréales utilise des cavités dans les arbres pour la nidification ou comme abris (approximativement 37 espèces - Darveau et Desrochers 2001). Des réseaux d'utilisateurs de cavité ou « nest web » similaires aux réseaux trophiques sont formés à partir d'interactions interspécifiques entre les animaux dépendant de cavités (Martin et Eadie 1999). La ressource centrale, c'est-à-dire les cavités, est partagée selon une hiérarchie d'utilisateurs et de liens entre ces derniers (Blanc et Walters 2007). En forêt boréale, les excavateurs primaires sont les pics et ces derniers excavent généralement une cavité annuellement pour y nicher. Les utilisateurs secondaires de cavités sont un groupe diversifié : passereaux, oiseaux de proie, canards et mammifères qui dépendent des cavités, mais ne peuvent les excaver. Les excavateurs faibles peuvent creuser leurs cavités dans du bois très décomposé ou réutiliser des cavités (Martin et Eadie 1999). En Amérique du Nord, la grande majorité des cavités utilisées ne résultent pas de la dégradation des arbres, mais sont excavées par les pics (Raphael et White 1984, Martin et Eadie 1999, Aitken et Martin 2004, Blanc et Walters 2008a, Cooke 2009, Cadieux 2011, Cockle et al.

2011). La création de cavités par les pics est donc considérée comme un processus clé dans les communautés forestières (Bednarz et al. 2004).

Les excavateurs de cavités de grande taille tels que le Pic flamboyant (*Colaptes auratus*) et le Grand Pic (*Dryocopus pileatus*) sont identifiés comme espèces clés de voûte par plusieurs études (Bonar 2000, Aubry et Raley 2002, Martin et al. 2004, Blanc et Walters 2008a, Cooke 2009, Cadieux 2011). Entre autres, les cavités excavées par le Grand Pic sont significativement moins nombreuses que les autres types de cavités (Bonar 2000, Vaillancourt et al. 2008) et ceci limite les utilisateurs de ce type de cavité. Cet excavateur est le seul à pouvoir créer des cavités assez grandes (soit deux fois le volume des cavités du Pic flamboyant) pour abriter les plus gros des utilisateurs secondaires, tels que le Garrot à œil d'or (*Bucephala clangula*) ou le Garrot d'Islande (*Bucephala islandica*) (Bonar 2000, Darveau et Desrochers 2001, Aubry et Raley 2002, Evans et al. 2002, Martin et al. 2004, Vaillancourt et al. 2008, Cooke 2009, Vaillancourt et al. 2009).

À la base des réseaux d'utilisateurs de cavités se trouvent les arbres. Dans les écosystèmes forestiers où le peuplier faux-tremble est présent, cette essence est hautement sélectionnée comme arbre de nidification (Dobkin et al. 1995, Aitken et al. 2002, Martin et al. 2004, Cadieux 2011). Certaines études ont associé la préférence de cette essence à la présence d'infections par un champignon : la carie blanche du tremble (*Phellinus tremulae*) (Kilham 1971, Hart et Hart 2001, Jackson et Jackson 2004, Martin et al. 2004, Savignac et Machtans 2006, Blanc et Martin 2012, Cooke et Hannon 2012). De même, les arbres utilisés par les excavateurs en forêt boréale résineuse sont généralement infectés par une carie du coeur de l'arbre (Goggans et al. 1989, Pechacek et d'Oleire-Oltmanns 2004).

Les arbres morts et sénescents sont d'importants réservoirs alimentaires pour plusieurs espèces d'oiseaux insectivores dont l'importance de ce rôle est accentuée en

hiver. La plupart des espèces de pics se nourrissent d'arthropodes et s'alimentent sur des arbres sénescents ou morts (Mikusiński 2006, Nappi et al. 2015). Ils se spécialisent selon l'essence, le diamètre et l'état de dégradation des arbres (voir Nappi et al. (2015) pour une étude détaillée dans notre région d'étude). Les pics boréaux, le Pic à dos noir et le Pic à dos rayé sont particulièrement spécialisés sur les arbres résineux de grand diamètre récemment morts (Darveau et Desrochers 2001, Imbeau et Desrochers 2002, Nappi et al. 2015). Le Pic à dos noir se nourrit exclusivement sur des arbres morts où il trouve des insectes foreurs phytophages (*Cerambicidae*) alors que le Pic à dos rayé se nourrit d'insectes xylophages sous l'écorce tant sur des arbres sénescents que morts (*Scolitidae*) (Murphy et Lehnhausen 1998, Saint-Germain et al. 2007, Nappi et al. 2015). Le Pic mineur (*Picoides pubescens*), le Pic maculé (*Sphyrapicus varius*), le Pic chevelu (*Picoides villosus*), et le Grand Pic s'alimentent principalement d'arthropodes retrouvés sur des essences feuillues et résineuses principalement retrouvées en forêt mixte. L'état de dégradation des arbres d'alimentation diffère selon les espèces, mais celles-ci utilisent en moyenne plus d'arbres vivants que ne le font les pics boréaux (Nappi et al. 2015).

Peu d'information existe sur l'utilisation d'arbres morts pour le tambourinage par les pics. Par contre, Imbeau et Desrochers (2002) caractérisent l'utilisation de ces arbres pour le Pic à dos rayé. Les arbres de tambourinage utilisés par les pics ont un grand diamètre, sont morts, creux et secs afin d'avoir les meilleures qualités de transmission sonore (Eberhardt 1997, Darveau et Desrochers 2001, Imbeau et Desrochers 2002).

Rôle des vieilles forêts résineuses dans l'apport de bois mort pour la faune cavicole en pessière à mousses

On ne sait que très peu de choses sur la capacité des vieilles forêts de pessière à mousses quant à leur capacité à offrir de conditions d'habitats adéquates pour les oiseaux associés au bois mort. Selon des études effectuées dans l'ouest de l'Amérique

du Nord, la distribution du bois mort en forêt tempérée de conifères suivrait une forme de «U» où une grande abondance de chicots serait présente suite au feu, suivi par une diminution constante de bois mort dans les forêts jeunes et matures et finalement, suivi par une abondance croissante dans les vieilles forêts (Harmon et al. 1986). Cependant, peu d'études ont été effectuées dans l'est de l'Amérique du Nord dans les forêts boréales de conifères où les diamètres des arbres sont considérablement plus faibles. Harper et al. (2005) proposent que cette forme ressemble davantage à un «J» inversé dans les forêts boréales de l'est de l'Amérique du Nord et que dans les pessières à mousses susceptibles à l'entourbement, on distingue même une abondance décroissante de bois mort dans les très vieilles forêts. En accord avec ceci, Drapeau et al. (2002) rapportent, dans une des seules études portant sur l'apport de bois mort pour les oiseaux cavicoles effectuée en pessière à mousses de l'ouest du Québec, que les très vieilles forêts (> 200 ans) ne joueraient pas un rôle clé dans l'apport d'un substrat adéquat à l'excavation de cavités par les oiseaux cavicoles. Cependant, nous ne disposons pas de données sur la distribution des espèces cavicoles le long d'un gradient d'âge et de structure forestière en pessière à mousses qui traduise les changements fins de structure de la végétation décrits dans Harper et al. (2005). À ce jour, aucune étude n'a examiné la contribution relative des forêts âgées encore productives, de celles en voie de paludification ainsi que des forêts paludifiées quant à la disponibilité du bois sénescent et mort ainsi que de la réponse des oiseaux associés à ce dernier. Ces forêts représentent pourtant une proportion non négligeable du domaine de la pessière à mousses.

Les forêts mixtes isolées en pessière à mousses, des oasis de biodiversité ?

Les forêts mixtes se raréfient considérablement du sud au nord de la forêt boréale, partant de grands massifs dans le domaine de la sapinière à bouleau blanc qui se fragmentent pour ne composer qu'une très faible proportion du domaine de la pessière à mousses. Les forêts mixtes seraient néanmoins hautement sélectionnées par

plusieurs espèces de vertébrés. Cheveau et al. (2013) ainsi que Potvin et al. (2000) rapportent que ces endroits seraient possiblement clés pour les populations de martre. De plus, Crête et Courtois (1997) rapportent que les forêts mixtes, même s'ils représentent que < 5 % de la forêt en pessière à mousses sont grandement sélectionnés par les orignaux comme site d'alimentation. Malgré leur isolement dans les grandes matrices résineuses, on ignore si ces îlots sont des habitats importants pour la faune cavicole dans le domaine bioclimatique de la pessière à mousses. À notre connaissance, aucune étude n'a abordé cette question.

L'aménagement forestier et les pics comme indicateurs de diversité

À l'échelle mondiale, les coupes forestières industrielles et la transformation des paysages forestiers en paysages agricoles ont causé d'importantes baisses de populations ainsi que des diminutions dans l'aire de répartition pour plusieurs espèces de pics (Mikusiński 2006, Winkler et al. 2010). Les espèces de grande taille sont particulièrement touchées, vu leur grand domaine vital et leur dépendance aux arbres de grand diamètre pour leur reproduction ou comme refuges (Mikusiński 2006).

En forêt boréale, l'aménagement forestier conventionnel à courtes révolutions tend à normaliser les classes d'âges des peuplements ce qui contribue à considérablement rajeunir la moyenne d'âge des paysages forestiers (Franklin et Forman 1987, Spies et al. 1994, Niemi et al. 1998, Cyr et al. 2009), qui est maintenant significativement plus basse que celle des paysages naturels perturbés par les feux (Bergeron et al. 2001, Bergeron et al. 2004, Cyr et al. 2009). Ce rajeunissement des paysages forestiers n'est pas sans conséquence sur l'abondance et la répartition de plusieurs des espèces de pics ayant le rôle clé d'excavateurs de cavités dans les forêts âgées tant mixtes (Drapeau et al. 2000, Hobson et Bayne 2000, Savignac et Machtans 2006, Schieck et Song 2006, Cooke 2009, Cadieux 2011) que résineuses (Imbeau et Desrochers 2002). En réponse à cet enjeu de rajeunissement des mosaïques forestières aménagées,

plusieurs chercheurs ont proposé le concept d'aménagement écosystémique, une approche d'aménagement forestier qui s'inspire des perturbations naturelles (Gauthier et al. 2008b). Un des principaux objectifs de cette approche est le maintien de la structure d'âge et de la proportion des différents types de peuplements qui sont observés sous un régime de perturbations naturelles (Gauthier et al. 2008a). Cette approche de filtre brut se base sur la prémisse que les espèces occupant un écosystème auraient évolué et se seraient adaptées aux régimes de perturbations de ce dernier (Hunter et al. 1988, Gauthier et al. 2008b). L'évaluation de la capacité de l'approche écosystémique à maintenir des éléments importants de la diversité biologique en forêt boréale passe par le suivi d'espèces indicatrices associées aux habitats les plus affectés par l'aménagement des forêts (Drapeau et al. 2008). Le suivi des espèces dépendantes du bois sénescent et mort et, plus particulièrement, d'espèces clés de voûte comme les pics, s'avère donc crucial pour l'évaluation de la mise en place de l'aménagement écosystémique.

Par ailleurs, plusieurs chercheurs et aménagistes forestiers recommandent l'utilisation ou utilisent le Grand Pic comme espèce parapluie ou comme espèce indicatrice des vieilles forêts (McClelland et al. 1979, Bull et al. 1992, Blanchette 1996, McLaren et al. 1998, McClelland et McClelland 1999, Savignac et al. 2000, Aubry et Raley 2003, Lemaître et Villard 2005, Cheveau 2015). La conservation de l'habitat du Grand Pic serait aussi bénéfique pour de multiples autres espèces vu que cette espèce est très exigeante tant pour ses arbres de nidification que pour les arbres d'alimentation. Par contre, nous n'avons répertorié aucune étude publiée avec révision par des pairs qui vérifie de manière empirique en quoi le Grand Pic constitue bel et bien une espèce parapluie.

Objectifs de la thèse

La forêt boréale de l'est de l'Amérique du Nord comprend d'importants gradients de productivité et de composition forestière : des pessières à mousses qui dominent largement la composition forestière, mais qui sont souvent affectées par la paludification, aux forêts mixtes dominées ou co-dominées par le peuplier faux-tremble qui se raréfient considérablement du sud vers le nord de la forêt boréale, mais qui ont une productivité nettement supérieure. Les oiseaux associés au bois mort tel que les pics sont répartis dans le territoire boréal parmi ces importantes sources de productivité forestière et de recrutement de bois mort et sénescent (Angelstam et Mikusiński 1994). Par contre, notre connaissance et notre compréhension de cette distribution s'avèrent incomplètes. En pessière à mousses de l'est de l'Amérique du Nord, ces oiseaux sont potentiellement limités par l'abondance d'arbres de nidification et d'alimentation adéquats. Cette thèse a comme objectif d'approfondir nos connaissances fondamentales sur l'écologie, dont une compréhension accrue du rôle joué par le bois mort et sénescent dans la diversité fonctionnelle de l'écosystème boréal. De plus, selon une perspective appliquée, cette thèse vise à développer d'un modèle de qualité d'habitat multi-espèces.

Dans le premier chapitre, nous explorons la relation que la faune cavicole entretient avec l'habitat forestier en pessière à mousses. Plus précisément, nous examinons le rôle des vieilles forêts dans l'apport de bois sénescent et mort et l'importance de cette ressource pour l'occurrence et l'alimentation par l'avifaune associée au bois mort. Les vieilles forêts boréales sont des habitats clés pour le recrutement à long terme d'arbres morts de grand diamètre. Par contre, la paludification des vieilles forêts de pessière à mousses réduit sévèrement la productivité forestière et, par conséquent, la production de bois sénescent et mort. Malgré l'importance de ce phénomène, très peu d'études portent sur les effets de la paludification sur la distribution des oiseaux associés au bois sénescent et mort (Drapeau et al. 2003). Les implications de ces

résultats pour la priorisation des habitats à conserver dans les paysages aménagés sont importantes ; les vieilles forêts n'ont probablement pas toutes la même valeur en ce qui concerne la conservation de la diversité aviaire en pessière à mousses.

La contribution des forêts mixtes isolées à la communauté cavicole dans le paysage résineux de la pessière à mousses est méconnue, mais l'isolement de ces habitats devrait affecter leur occupation par les espèces cavicoles. Le deuxième chapitre porte sur l'influence de la disponibilité des arbres adéquats à l'excavation de cavités sur la structure des réseaux d'utilisateurs de cavités. L'excavation de cavités de nidification par des excavateurs clés dans le paysage peut avoir de grandes répercussions sur la nidification d'utilisateurs secondaires de cavités. Les grands utilisateurs secondaires de cavités tels que le Garrot à oeil d'or (*Bucephala clangula*) sont particulièrement dépendants de grandes cavités qui sont quasi exclusivement excavées par le Grand Pic. Cependant, le processus d'excavation de grandes cavités en pessière à mousses de l'est de l'Amérique du Nord est fortement contraint par le faible diamètre des arbres. Depuis une dizaine d'années, plusieurs études ont été effectuées sur la structure des réseaux d'utilisateurs de cavités (Martin et Eadie 1999, Martin et al. 2004, Blanc et Walters 2007, Blanc et Walters 2008a, Blanc et Walters 2008b, Bavrlic 2009, Cooke 2009, Cadieux 2011). La grande majorité de celles-ci sont effectuées en forêt mixte. À notre connaissance, aucune étude en forêt boréale ne traite de réseaux d'utilisateurs de cavités en paysage dominé par des forêts de conifères comme la région de la pessière à mousses.

En aménagement écosystémique, il est important de disposer d'indicateurs qui déterminent la capacité des stratégies d'aménagement à maintenir la diversité biologique. Ces indicateurs, de type évaluatif, vérifient l'hypothèse d'une relation entre l'action d'aménagement et son effet sur la diversité biologique (Drapeau et al. 2008). Avoir des cibles d'aménagement qui permettent la cohabitation de l'aménagement forestier et le maintien des réseaux d'utilisateurs de cavités riches et

complexes en forêt boréale sous-tend l'identification des habitats clés à préserver dans les paysages aménagés. Ces habitats doivent répondre aux exigences des espèces cavicoles tant sur le plan des gites de reproduction que des arbres d'alimentation. Le troisième chapitre a pour objectif d'évaluer l'efficacité d'utiliser le Grand Pic comme une espèce parapluie pour la conservation de l'ensemble de la faune cavicole. Cette espèce est souvent qualifiée d'espèce parapluie par des chercheurs et des aménagistes forestiers, mais nous n'avons répertorié aucune étude publiée avec révision par des pairs ayant vérifié cet énoncé avec des données empiriques. Nous testons l'hypothèse que la sélection d'habitat effectuée par le Grand Pic engloberait la sélection d'habitat de la majorité des espèces cavicoles. Par conséquent, la conservation de l'habitat du Grand Pic serait aussi bénéfique à de multiples autres espèces cavicoles en forêt boréale.

CHAPITRE 1

ARE OLD BOREAL FORESTS A SAFE BET FOR THE CONSERVATION OF THE AVIFAUNA ASSOCIATED WITH DECAYED WOOD IN EASTERN CANADA?

1.1 Résumé

Les vieilles forêts boréales sont considérées comme des habitats de qualité pour l'avifaune associée au bois sénescent et mort. Cependant, la quantité et la qualité des arbres morts et sénescents sont probablement influencées par d'importants changements latitudinaux dans la composition et la productivité forestière partant des forêts boréales mixtes du sud aux forêts résineuses nordiques. Nous avons mesuré l'occupation de l'habitat des oiseaux cavicoles et corticoles dans les vieilles forêts à la zone de transition entre la forêt boréale mixte et résineuse du Nord-Ouest du Québec. En utilisant de la repasse de chants et de tambourinage ainsi que des marques récentes d'alimentation sur les arbres, nous avons mesuré l'occurrence de 11 espèces d'oiseaux dans 85 peuplements de forêts mixtes et résineuses non aménagées le long d'un gradient d'âge. Bien qu'ils ne représentent que 4 % du couvert forestier dans la région d'étude, les vieilles forêts mixtes (> 90 ans) étaient de loin les plus utilisées par l'avifaune associée au bois mort. Dans les peuplements dominés par les conifères ces oiseaux ont montré une réponse modale au vieillissement et à la réduction de la productivité forestière atteignant le maximum dans les peuplements de 160 ans pour ensuite redescendre. Les peuplements paludifiés qui composaient plus de 40 % du paysage ont étés associés à une richesse d'espèces significativement plus pauvre d'oiseaux cavicoles et corticoles. La diversité structurale des tiges (diversité des stades de dégradation et du diamètre des arbres) était la variable qui a le mieux expliqué la richesse d'espèces de ce groupe fonctionnel tandis qu'à l'échelle de l'espèce individuelle, de grandes quantité et qualité de bois sénescent et mort dans les peuplements ont le mieux expliqué l'occurrence des espèces et l'abondance de traces d'alimentation des pics. Les traces d'alimentation du Pic à dos noir (*Picoides arcticus*) et le Pic à dos rayé (*Picoides dorsalis*) ont atteint leur abondance maximale dans les vieux peuplements productifs résineux. Les traces d'alimentation des autres pics étaient principalement trouvées en forêts mixtes. Les efforts de conservation de l'avifaune associée au bois mort devraient être priorisés dans les vieux peuplements productifs autant résineux que mixtes. Cependant, notre étude désigne les vieilles forêts mixtes comme des habitats qui méritent une préoccupation particulière pour ce groupe fonctionnel d'oiseaux.

1.2 Abstract

Old boreal forests are considered quality habitats for birds associated with decaying and dead trees. However, the quantity and quality of these structural attributes in old forest stands are likely to be influenced by important latitudinal changes in tree species composition and productivity from the southern boreal mixed to the northern coniferous forests. We measured habitat occupancy of cavity and bark nesting birds in old forests when the boreal forest landscape shifts from a mixed to a dominant coniferous matrix in the Clay Belt of Québec and Ontario, a region where paludification dominates. Using playback calls, songs, and recent woodpeckers' foraging signs on trees, we measured the occurrence and foraging habitat use of 11 bird species associated with deadwood in 86 unmanaged forest stands along a forest age gradient in both mixed and coniferous stands. In coniferous stands dominated by black spruce, deadwood birds showed a modal distribution in response to the aging of black spruce forests that reached a peak in stands of 160 years and then declined. Unproductive paludified stands, which made up more than 40 % of our study area, were associated with a significantly lower species richness of deadwood birds. At the opposite, although they represented less than 4 % of the forest cover in our study area, old boreal mixedwood forests (> 90 years) were highly utilized habitats by deadwood birds. Structural diversity of trees (diversity of degradation stages and diameter of trees) was the variable that best explained species richness of this functional group of birds whereas at the individual species level, the quantity and quality of dead trees (degradation and size) in stands best explained species occurrence and abundance of foraging signs. Conservation efforts for deadwood birds should focus on old productive stands of both mixed and coniferous composition. However, our study pinpoints old mixedwood stand as habitats of special concern given their disproportionate importance for deadwood birds in northern boreal forests.

1.3 Introduction

In old boreal forests, decaying and dead wood represent key structural attributes for biodiversity (Stokland et al. 2012). Birds that use decaying and dead wood for nesting represent a major component of old forest bird communities (Angelstam and Mikusiński 1994, Niemi et al. 1998, Imbeau et al. 1999, 2001, Schmiegelow and Mönkkönen 2002, Drapeau et al. 2003, 2009, Schieck and Song 2006). They have been proposed to be general indicators of old forests' biodiversity (fungi, insects, birds, mammals) (Mikusiński et al. 2001, Virkkala 2006, Drever et al. 2008, Roberge et al. 2008). Within this focal group, woodpeckers are keystone species and ecosystem engineers since they produce most of the cavities that are used by a wide range of other vertebrates that cannot create their own cavities for roosting and reproduction (Aubry and Raley 2002, Bednarz et al. 2004, Martin et al. 2004, Cockle et al. 2012, Tremblay et al. 2015a).

In recent years, studies on cavity-nesting communities in subalpine and boreal forests across Canada have found that large decaying and dead deciduous trees, particularly trembling aspen (*Populus tremuloides*), are the primary nesting substrates for most cavity users (Martin et al. 2004, Cadieux 2011, Cooke and Hannon 2012, Ouellet-Lapointe et al. 2012). Whereas decaying and dead trembling aspens are found in a wide range of old forest cover types in the southern boreal forest (Bergeron and Charron 1994), their availability may be reduced at more northerly latitudes due to changes in natural disturbance regimes linked with fire size and severity (Bergeron et al. 2004), which affects tree species composition of the forest cover (Gauthier et al. 2000). In addition, in some regions, such as in northwestern Québec and northeastern Ontario, northerly dominant black spruce stands are prone to paludification, a process of gradual conversion of a mesic forest to a forested peatland through the accumulation of organic material and water table rise (Taylor et al. 1988, Simard et al. 2007). Old black spruce stands thus present a wide spectrum of stand structures

(Harper et al. 2002, 2003) ranging from increased vertical heterogeneity to extensive open canopy with smaller sized trees where the oldest stands may resemble bogs (Lecomte et al. 2006a, 2006b).

Preliminary results on bird communities in black spruce forests of these regions have shown that species associated with canopy cover (foliage gleaners, canopy nesters) and old decaying trees (bark foragers, cavity nesters) become rare and are replaced by open habitat specialists (shrub nesters) in very old black spruce stands (> 200 years since last fire), as they are not evolving into more complex vertical structures but are more simplified with an extreme canopy openness (Drapeau et al. 2003). Such turnover in bird community composition depicts a broad change in forest structure between recently old (100 – 200 years) and very old forests (> 200 years) in landscapes prone to paludification. Clear understanding of the degree to which deadwood birds track structural changes in old black spruce forests is, however, lacking.

The latitudinal changes in structure and composition of old forests may thus diminish their role in providing key habitat conditions to deadwood bird species. Increased knowledge on how regional distribution patterns of this focal group of bird species changes over the natural transition from mixed to a conifer-dominated matrix in the boreal forest is thus critical to develop conservation planning of biodiversity in old stands in managed landscapes. This is still the case as commercial timber harvesting is unfolding in the north with extensive implementation of short-rotation even-aged management favoring an increase in the proportion of early-seral habitats and concurrent reduction in late-seral habitats even though ecosystem-based management mitigates this change (Gauthier et al. 1996, Bergeron et al. 2002, 2007).

In this study, we evaluate the importance of old boreal forests for deadwood birds when the boreal forest shifts from a mixed to a conifer-dominated matrix in the Clay

Belt region of Québec and Ontario which is greatly affected by paludification. We hypothesize that old forest stands in this part of the boreal forest provide limited nesting and foraging conditions, reducing deadwood birds species richness patterns. More specifically, we make the following predictions at the community and individual species' levels. At the community level, we predict that in black spruce stands there will be a modal distribution of deadwood birds species richness and foraging habitat use, increasing along the age and structure gradient and declining as forests are affected by paludification. Second, since they are strongly isolated in the conifer-dominated forest matrix, boreal mixedwood stands will not have a higher species richness or foraging habitat use than black spruce stands. Third, the quantity and structural diversity of live and dead trees (size and degradation) will be the best predictor of deadwood birds' species richness and abundance of foraging signs. Fourth, at the species level, deadwood birds' occurrence and foraging habitat use patterns will translate into individualistic responses associated with specific structural attributes of live and dead trees.

1.4 Methods

1.4.1 Study area

The study was conducted in northwestern Québec in the black spruce-moss bioclimatic domain (Robitaille and Saucier 1998). This region is part of a broad physiographic unit, the clay belt, which is located south of James Bay and extends across northern Québec and Ontario. The flat topography of the region originates from clay deposits left by proglacial lake Ojibway (Vincent and Hardy 1977, Veillette 1994). The study region is characterized by lower altitude (250 m) and the abundance of wetlands.

To obtain a representative sample of the range of forest cover types in the boreal forest of northwestern Québec, we sampled a large area of Québec's Clay Belt

(Figure 1.1). Specifically, we selected study sites in two regions, north of La Sarre (48°48'37.5"N 79°12'34.1"W) in the forest management units (FMU) 8551 and north of Lebel-Sur-Quévillon (49°03'18.1"N 76°59'42.2"W) in the FMU 8763 that differ in their topography and therefore their potential for paludification. The average annual temperature was 0.0 °C with an average annual precipitation of 909 mm, taken at the nearest weather station in Joutel, Québec, 1981-2010 (49°27′ N; 78°18′ W) (Environment Canada, 2016).

1.4.2 Site selection

We selected sites along a gradient of forest age, composition and structure, combining information from digital forest cover maps (MRNF 2011) and field validation. Coniferous black spruce dominated stands were selected using digital forest cover maps and time since last fire estimates from two data sources. First, a study of fire history reconstruction provided extensive information on past historical fire events on a regional scale (Bergeron et al. 2004). Second, precise estimates of forest stand age were provided by detailed local scale dendrochronological analysis of stems (see Chaieb et al. 2015 for details). We selected 43 black spruce dominated stands aged 61-215 years : 60-90 years (n=8), 90-120 years (n=11), 120-160 years (n=14), 160-215 years (n=10). We enlarged this structural gradient by adding 21 stands that were in the process of paludification (n=7) and paludified (n=14). For the former, we selected stands 83-460 years considered forested in the first regional forest inventory that were later classified as bogs in the third regional forest inventory (MRNF 1994, 2009). Paludified stands (between 75-3849 years) were considered as bogs on digital forest cover maps. We selected 22 mixedwood stands dominated or co-dominated by trembling aspen and from two age-class categories provided on the digital forest cover maps 70-90 years (n=11) and > 90 years (n=11). In each stand we positioned one playback station (total n=86 stations) at least 100 m away from the edge of the stand and separated by > 400 m.

1.4.3 Habitat sampling

We positioned three 400 m^2 sampling plots within a 100 m radius centered on the location of the playback stations to measure woodpecker foraging signs and to characterize the vegetation. One plot was positioned at the playback station whereas the two others were positioned 60 m away on randomly chosen cardinal directions. Precise measures were taken for every tree larger than 10 cm in DBH (diameter at breast height): tree species, degradation class and the presence or absence of woodpecker foraging signs. Tree degradation was classified based on visual appearance in 8 categories according to Imbeau et Desrochers (2002) (1 = alive and healthy > 95 % foliage; 2 = live but senescent, between > 20 % and 95 % foliage; 3 = dying < 20 % foliage; 4 = recently dead, no green foliage; 5 = hard wood, no dead foliage, no small twigs; 6 = hard wood, loose bark cover, broken top, > 50 % of original height; 7 = soft, decomposed wood, broken top with < 50 % of original height; 8 = stump, height < 2 m). Mean tree diameter and basal area per hectare were calculated combining all trees from the three vegetation plots. A 120 m transect was aligned with the center of the three plots to measure, at the point of intersection, the diameter and degradation of the deadwood on the ground. Downed deadwood volume (m^3/ha) was estimated for each stand with a formula developed by Van Wagner (1968). We measured the proportion of forest cover types at the landscape scale with digital forest cover maps (MRNF 2011) delimited by the forest management units of each region.

1.4.4 Bird sampling

The response to the playback calls in a 75 m radius was used to measure the occurrence of individual species and the species richness of our focal group comprised of eleven bird species: Yellow-bellied Sapsucker (*Sphyrapicus varius*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*Picoides arcticus*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker

(Dryocopus pileatus), Boreal Chickadee (*Poecile hudsonicus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), and Winter Wren (*Troglodytes hiemalis*) (Appendix A). The playback calls were comprised of one-minute calls and drumming for each species interspersed by one minute of silence. The sequence of calls was ordered by the species body mass from small to large. Each site was visited three times during the breeding period from the beginning of May to the end of June between 05:00 and 10:00 and during adequate weather conditions (no heavy rain or strong winds).

Even though playback methods may be more appropriate for detecting elusive species that have large home ranges such as woodpeckers, it nevertheless remains that birds may use our sampling sites without responding to playbacks. The presence of a woodpecker's recent foraging signs on trees may thus be considered as a complementary information that provides an index of foraging activity, and thus, of habitat use of our study sites. We recorded the presence and absence of 4 types of foraging signs on trees in the vegetation sampling plots that can be associated with 5 woodpecker species. Foraging signs were identified and associated with woodpecker species based on an intensive study conducted on the foraging behavioral ecology of woodpeckers in the same region (Nappi et al. 2015) (Appendix A). We distinguished recent foraging signs from older ones by the color and sharpness of the wood and only recent foraging signs are used in the analyses. The Yellow-bellied Sapsucker sapwells are easily identified by distinctive patterns of small rectangular holes organized in horizontal rows on live trees that are close to one another to form vertical chains (Eberhardt 2000) and not horizontal rows that are dispersed on the trunk as those of American Three-toed Woodpeckers (Bailey 2008). The Pileated Woodpecker foraging signs are also easily identified because they represent very large excavations in large senescent or dead trees often leading to carpenter ants galleries (Bull and Jackson 2011). The Hairy Woodpecker excavates small holes to find wood-boring beetles and forages mostly on deciduous trees (Nappi et al. 2015).

The Black-backed Woodpecker forages almost exclusively on dying or recently dead coniferous trees by mainly excavating small holes to find wood-boring beetles but may also forage by scaling bark for bark beetles (Tremblay et al. 2010, Nappi et al. 2015). The American Three-toed Woodpecker mostly scales bark and rarely excavates as it feeds on bark beetles (Leonard and David 2001, Nappi et al. 2015). Whereas identification of small foraging signs by the *Picoides* group (Hairy, Black-backed and American three-toed woodpeckers) can be separated on the basis of habitat types in which they are found (Nappi et al. 2015), our censuses are not based on visual observations of foraging birds. Therefore, to avoid over-interpretation on species identity, we did not assign excavations and bark scaling foraging signs to specific species. Small foraging signs for both bark scaling and excavation were thus combined into a single *Picoides* group (Hairy, Black-backed and American Three-toed woodpeckers).

1.4.5 Statistical analyses

We characterized habitats by variables known to be important for nesting and foraging requirements of the focal group of species under study (Martin et al. 2004, Cadieux 2011, Nappi et al. 2015), and which represented tree composition and productivity, the quantity of deadwood in the stand and the tree structural diversity (Table 1.1). Tree structural diversity was calculated using the Shannon-Weaver diversity index where our surrogate "species" corresponded to the combination of the degradation classes and the DBH of trees classified into categories (in 5 cm classes) for standing and downed trees (Harper et al. 2003). We used a theoretical-information approach using Akaike information criterion adjusted for small samples (AICc) to estimate if a model which included the habitat categories performed better than a null model, a model that included only the intercept (Burnham and Anderson 2002). We report the model's Akaike weight (w_i) which is the strength of evidence for each model (ratio of ΔAICc) and the null model's difference in AICc (ΔAIC_c) (Burnham and Anderson 2002, Mazerolle 2006). For example, a $\Delta AIC_c < 2$ suggests strong

support for the model, values between 3 and 7 suggest substantially less support whereas models with >10 ΔAICc are considered poorly supported by the data (Burnham and Anderson 2002, Mazerolle 2006). To model the relationships between habitat variables and habitat types, we used generalized linear models (GLMs) assuming a normal distribution for variables with normally distributed residuals and assuming a Poisson distribution for count data. Non-normally distributed variables were log transformed to fit the requirements or were analyzed with a Kruskal-Wallis test followed by Dunn's test with a Bonferonni correction with a significance level of 0.05. In the case of overdispersion, the quasi-likelihood Akaike information criterion was used. We calculated 95% confidence intervals through model averaging predictions with the R-package "AICcmodavg" version 2.0-3 (Mazerolle 2015). Statistically significant differences between habitat types, represented by different letter combinations, were calculated with model-averaging of effect size on group differences in which the confidence intervals were adjusted for multiple comparisons with the Bonferonni correction (Mazerolle 2015).

To analyze the patterns of distribution of deadwood birds, we compared the occurrence of individual species, species richness and the abundance of foraging signs on trees between habitat types. We used the same theoretical-information approach as discussed earlier.

We determined which habitat variables were the most influential for the occurrence of individual species, the species richness of deadwood birds, and the abundance of foraging trees by comparing a list of simple models composed of a single habitat variable (Table 1.1). We used a theoretical-information approach with Akaike information criterion adjusted for small samples (AIC_c) to compare candidate models and to select the most parsimonious (Burnham and Anderson 2002). Model averaging was used to calculate model averaged estimates where there were more than one variable per model as was the case for the individual species occupancy modeling that

included detection variables and habitat variables (see below). Model selection and averaging was performed using the R-package "AICcmodavg" version 2.0-3 (Mazerolle 2015). We report models having a AIC_c difference (ΔAIC_c) < 2 and the null model. The R-package "ggplot2" was used for graphics (Wickham 2009). Statistical analyses were conducted using the R version 3.2.3 (R Core Team 2015).

For individual species occurrences, we estimated playbacks site occupancy rates with the R-package "unmarked" using the single season occupancy model function (MacKenzie et al. 2002, 2006, Fiske and Chandler 2011). This method estimates the probability of detection of individual species to account for false absences. It allows for a greater accuracy in occupancy probability compared to the observed occurrence defined here as the presence or absence of a species in 3 visits at a site (MacKenzie et al. 2002). However, modeling occupancy probability with this technique does not perform well when species have very low detection probabilities (< 0.15) (MacKenzie et al. 2002). For this reason, we excluded species with a detection probability below this threshold from analyses for individual species occurrences. Possible variables influencing detection probability were defined as detection variables: the observers classified by experience (ExpObs; low and high), the time of the day (Minutes; number of minutes), wind strength (Wind; 3 categories) and the date (Julian days). To limit the number of parameters in habitat variable models, we first did a model selection procedure for selecting variables influencing detection probability. Models with only detection variables were compared to a model with only the intercept. To be used in the habitat variables models, the detection variables had to be among the best models (< 2 ΔAIC_c) and more supported than a model with only the intercept. Model fit was assessed by comparing the distribution of $\chi 2$ of the model to the distribution of $\chi 2$ obtained by parametric bootstraps with 10 000 iterations and models with a bad fit were not used in model selection (MacKenzie et al. 2006).

Species richness of deadwood birds and abundances of foraging trees' relationships between habitat types and habitat variables were modeled using generalized linear models (GLMs) assuming a Poisson distribution. In the case of overdispersion, the quasi-likelihood Akaike information criterion was used ($\Delta QAIC_c$) instead of the ΔAIC_c.

1.5 Results

1.5.1 Overall landscape patterns

At the landscape scale, 84 % of the forest cover in our study region was coniferous including old paludified coniferous forests and bogs which covered more than 40 % of our study area (Figure 1.2). Coniferous stands > 90 years were fairly well represented with 25 % of the forest cover (Figure 1.2). Mixedwood stands were scarcer with a total of 15 % of forest cover of which only 4 % were mixedwood stands older than 70 years (Figure 1.2).

1.5.2 Habitat characteristics

Composition and productivity differed strongly between black spruce stands, stands affected by paludification and mixedwood stands. Diversity of tree species and trembling aspen basal area were higher in mixedwood stands (Table 1.2). Black spruce basal area was higher in black spruce stands and lower in paludified stands and mixedwood stands (Table 1.2). Variables representing forest productivity, the total basal area and the DBH followed a similar pattern: the lowest values were found in paludified stands followed by stands undergoing paludification and black spruce stands and the highest values in mixedwood stands (Table 1.2). Mixedwood stands > 90 years had a significantly higher mean DBH than 70-90 years mixedwood stands (Table 1.2).

The quantity and size of deadwood differed significantly by habitat. Downed deadwood volume followed a modal distribution along the age and structure gradient in coniferous stands and was highest in > 90 years mixedwood stands but did not differ significantly from 70-90 years mixedwood stands (Table 1.2). The mean dead tree DBH was highest in mixedwood stands > 90 years (> 25 cm) followed by 70-90 years mixedwood stands which did not differ significantly from 90-120 years black spruce stands and 160-215 years black spruce stands (Table 1.2). Stands affected by paludification had the lowest mean dead tree DBH values (Table 1.2).

Densities of recently dead and highly degraded trees varied by habitat. The density of recently dead trees of 10-20 cm DBH only differed significantly between 90-120 years black spruce stands and paludified stands. The density of recently dead trees of > 20 cm DBH was highest in mixedwood stands > 90 years. However, these values were not significantly different from 70-90 years mixedwood stands and 90-120 years black spruce stands. Black spruce stands and stands affected by paludification had low densities of recently dead trees of > 20 cm DBH (Table 1.2). Densities of highly degraded trees of 10-20 cm DBH were highest in 70-90 years mixedwood stands and differed significantly from mixedwood stands > 90 years and paludified stands but not from other habitat types (Table 1.2). Densities of highly degraded trees of >20 cm DBH were significantly higher in mixedwood stands > 90 years. These densities were second highest in 70-90 years mixedwood stands but did not differ significantly from old black spruce stands (90-120 years) and 160-215 years black spruce stands.

The density of trees adequate for cavity excavation was highest in mixedwood stands (93.18 trees/ha). Mixedwood stands 70-90 years had the second-highest values but these did not differ significantly from 90-120 years black spruce stands.

Tree structural diversity followed a modal distribution along the age and structure gradient in black spruce stands and was highest in mixedwood stands (Table 1.2).

Paludified stands had the lowest tree structural diversity, which was not significantly different, however, from stands undergoing paludification and 60-90 years black spruce stands (Table 1.2). Black spruce stands 160-215 years had a significantly higher tree structural diversity than 60-90 years black spruce stands (Table 1.2).

1.5.3 Patterns of distribution of deadwood birds

All species responded to the playback calls. However, for most species, detection probabilities and occurrences were too low to model adequate occupancy probabilities across the 8 habitat types. (Table 1.3). Hence, we present means of the observed occurrences by habitat types (Figure 1.3). The Black-backed Woodpecker and the American Three-toed Woodpecker were mainly distributed in the coniferous stands whereas the other woodpecker species were mostly observed in mixedwood stands (Figure 1.3). The Downy Woodpecker, and the Yellow-bellied Sapsucker, occurred almost exclusively in mixedwood stands (Figure 1.3). Non-woodpecker species were distributed throughout black spruce and mixedwood stands but had their highest occurrence in 90-215 years black spruce stands and mixedwood stands > 90 years (Figure 1.3).

Species richness of deadwood birds was highest in mixedwood stands and followed a modal distribution in black spruce stands ($w_i = 1$, null model's $\Delta AIC_c = 54.31$; Figure 1.4). Mixedwood stands > 90 years had the highest species richness but did not differ significantly from 70-90 years mixedwood stands and 120-160 years black spruce stands. While there was a trend of higher species richness in black spruce stands > 90 years, only 120-160 years black spruce stands had significantly higher species richness than 60-90 years black spruce stands whereas paludified stands had the lowest species richness (Figure 1.4).

Throughout our 86 bird sampling sites, we inspected 8748 trees for 4 types of woodpecker foraging signs and found 644 trees with recent woodpecker foraging

signs (474 trees with *Picoides* foraging excavations, 203 with *Picoides* bark scaling, 45 trees with Pileated Woodpecker foraging excavations and 39 trees with Yellow-bellied Sapsucker sapwells). Overall, woodpeckers' foraging signs were well represented in mixedwood stands > 90 years whereas 60-90 years black spruce and paludified stands had the lowest densities of foraging trees (Figure 1.5). Trees with *Picoides* bark scaling signs were most abundant in 90-215 years black spruce stands (w_i=1, null model's $\Delta QAIC_c$ = 174.4; Figure 1.5). These stands did not differ significantly from stands undergoing paludification and mixedwood stands (Figure 1.5). However, they had significantly higher densities than 60-90 years black spruce stands and paludified stands (Figure 1.5). *Picoides* foraging excavations were most abundant in mixedwood > 90 years stands but these abundances were not significantly higher than abundances in black spruce stands 90-120 years and 160-215 years (w_i=1, null model's $\Delta QAIC_c$ = 21.65; Figure 1.5). Black spruce stands 60-90 years and paludified stands had the lowest values (Figure 1.5). Even though Pileated Woodpecker's foraging signs densities were higher in mixedwood stands > 90 years, they did not differ significantly from 70-90 years mixedwood stands, 90-120 years black spruce stands and 160-215 years black spruce stands (w_i=1, null model's ΔAIC_c = 14.62) (Figure 1.5). Yellow-bellied Sapsucker's sapwell trees (w_i=1, null model's ΔAIC_c = 54.09) were almost exclusively found in mixedwood stands (Figure 1.5).

1.5.4 Influence of habitat variables on species richness and individual species of deadwood birds

Species richness was best explained by a positive relationship with tree structural diversity and no other model was closely competing (w_i = 0.95, β = 0.43, 95% CI = 0.28-0.58, null model's $\Delta QAIC_c$ = 26.79).

For individual species, habitat and detection variables were identified as having an important effect on site occupancy (Table 1.4). The Yellow-bellied Sapsucker's site

occupancy was strongly related to tree species diversity whereas no other models were competing (Table 1.4). For this species, detection variables were not found to have a significant effect on the detection probability (null model's ΔAIC_c =0.41). Multiple competing models best explained site occupancy of the Downy Woodpecker: a high volume of deadwood, a high mean DBH and a high total tree basal area (Table 1.4). However, for the Downy Woodpecker, detection variables did not explain more than the model with only the intercept (null model's ΔAIC_c = 0.00). The Northern Flicker's site occupancy was not strongly associated with any habitat variables but its detection was significantly higher in early days of surveys (negative relationship with julian days ; Table 1.4). The Red-breasted Nuthatch site occupancy was associated with a high total tree basal area and its detection probability was positively influenced by the observer's experience (Table 1.4). There was no significant association between habitat variables and the Brown Creeper's site occupancy, whereas its detection was influenced by the observer's experience (Table 1.4). The Winter Wren's site occupancy was associated with high volume of downed deadwood and its detection was positively influenced by the observer's experience and negatively associated with late morning surveys (Table 1.4).

1.5.5 Influence of habitat variables on abundances of trees with foraging marks

The abundance of the four types of foraging signs on trees was strongly associated with specific habitat variables and null models were not closely competing (Table 1.5). The abundance of trees with *Picoides* bark scaling was associated with high densities of recently dead trees with a DBH of 10-20 cm. The abundance of trees with *Picoides* foraging excavations was associated with a high tree structural diversity (Table 1.5). Abundance of trees with Yellow-bellied Sapsuckers sapwells was best explained by tree species diversity (Table 1.5). The abundance of trees with Pileated Woodpecker foraging signs was best explained by two competing models, the mean tree diameter, and the tree structural diversity (Table 1.5).

1.6 Discussion

We hypothesized that birds associated with old boreal forests and deadwood would face increasing challenges in the black spruce forest of eastern Canada, due to the reduction in the amount of old mixedwood stands, which provide large deciduous trees for nesting or foraging requirements, and the corresponding increase of conifer stands with smaller trees, predominantly black spruce. Furthermore, in the Clay Belt region of Québec and Ontario, this availability of large decaying and dead trees becomes even lower since old black spruce stands are prone to paludification leading to a low stand productivity (Harper et al. 2005, Simard et al. 2007). Setting priorities for forest management and conservation of deadwood birds thus becomes a difficult task in such a context of reduced decayed wood availability and accordingly lower deadwood birds' species richness. Our results support several of the predictions linked with this hypothesis. For instance, we found that species richness of deadwood birds and their habitat use followed a modal distribution along the age and structure gradient in black spruce forests reaching the lowest values in paludified stands, thus indicating that not all old black spruce forests are good targets for the conservation of deadwood birds (prediction 1). However, contrary to our prediction, boreal mixedwood stands were surprisingly important habitats for deadwood birds even though they were rare and isolated in the conifer-dominated black spruce matrix (prediction 2). As we predicted, tree structural diversity was the best response variable for explaining species richness of deadwood birds (prediction 3), whereas at the species level, species-specific key tree attributes shaped deadwood birds' responses to structural changes in both black spruce and mixedwood forest stands (prediction 4).

1.6.1 Black spruce forests

In black spruce forests, the lowest values for species richness of deadwood birds were found at the beginning of the age and structure gradient, in 60-90 years black spruce stands and at the end of the gradient, in paludified stands. Individual species occurrences and densities of foraging trees were also generally lower in these habitats. While these two habitat types contrasted in productivity (60-90 years black spruce stands having higher mean DBH and tree basal area), they shared the common characteristics of having low quantities of deadwood and tree structural diversity suggesting low habitat quality for our focal group of birds. Other studies have found that mature boreal coniferous stands have lower species richness of birds associated with deadwood compared to older coniferous stands (Imbeau et al. 1999, Imbeau et al. 2001, Drapeau et al. 2003, Schieck and Song 2006), but very few studies have looked at the effect of paludification on deadwood birds use of old forests. Drapeau et al. (2003) conducted a preliminary study indicating that paludification in old boreal coniferous forests may affect deadwood birds. Our study provides, however, the first quantitative assessment of this relationship with data on both breeding and foraging habitat use by this focal group of birds.

In boreal forests, the accumulation of soil organic matter (paludification) has the potential to reduce forest productivity over time (Prescott et al. 2000). This paludification process can be edaphic (topography and drainage) but it can also be driven by forest succession only, regardless of position or slope (Simard et al. 2007). This affects the capacity for a stand to maintain larger trees, which in turn contributes to the recruitment of large decaying and dead trees in aging stands (Harper et al. 2005). Truncation in the recruitment of such attributes in old paludified stands is likely to affect nesting and foraging substrates for deadwood birds (Drapeau et al. 2009). While this paludification process is more severe in some regions of the boreal forest, as is the case in our study area, its effects may nevertheless be felt throughout the boreal forest at varying degrees (Prescott et al. 2000, Simard et al. 2007). Hence,

the modal distribution of deadwood birds in aging black spruce forests may not only reflect the extensive occurrence of paludification in the Clay belt region, but also reveal a potential trajectory of habitat occupancy by deadwood birds in old black spruce forest for other regions less prone to large-scale paludification.

Black spruce stands 90-215 years were associated with higher species richness of deadwood birds and higher *Picoides* foraging habitat use. Higher availability of deadwood and tree structural diversity explains higher species richness in these stands. For example, the Winter Wren, which had a high occurrence in these stands, was strongly associated with high downed deadwood volume reflecting its use for woody debris or uprooted trees to nests (Bent 1948). Likewise, high values of tree structural diversity and high densities of recently dead trees of 10-20 cm DBH best explained densities of foraging excavations and bark scaling by the *Picoides* group, respectively. Black-backed and American Three-toed woodpeckers select large recently dead coniferous trees for foraging (Imbeau and Desrochers 2002, Nappi et al. 2003, 2015, Gagné et al. 2007, Tremblay et al. 2010, 2015a). It is likely that these two species are the main contributors to the *Picoides* group for both excavations and bark scaling signs in black spruce stands > 90 years, even though they showed low values of observed occurrences and detection probability when using playbacks. Their very low densities and large home ranges in unburned stands (Goggans et al. 1989, Tremblay et al. 2009) in comparison with high densities and small home ranges found in recent burns, particularly for the Black-backed Woodpecker (Nappi and Drapeau, 2009), underlines the interest of using fresh foraging signs data as a measure of habitat use by these uncommon species.

1.6.2 Mixedwood forests

An important result of our study is how mixedwoods were key habitats for deadwood birds in black spruce landscapes notwithstanding their isolation and marginal regional abundance. Mixedwood stands > 90 years harbored the highest species richness of

deadwood birds, although they did not significantly differ from mixedwood stands 70-90 years and black spruce stands 120-215 years. Mixedwood stands had high forest productivity (mean tree DBH, total basal area) contrasting sharply with the lower productivity of black spruce stands and even more for stands affected by paludification. Notably, mixedwood stands > 90 years had the highest mean DBH of living and dead trees and had the highest densities of trees considered adequate for cavity excavation, i.e., large senescent trembling aspen with fungal conks of *Phellinus tremulae* (Cadieux 2011, Cooke and Hannon 2012). Furthermore, large decaying trembling aspen are also strongly selected for foraging by multiple woodpecker species (Nappi et al. 2015). Hence, not surprisingly our highest densities of Pileated Woodpecker and Yellow-bellied Sapsucker foraging signs were found in mixedwood stands, particularly in mixedwood stands > 90 years. While these two woodpeckers strongly select large old and senescent trembling aspen for their nesting cavities, their foraging signs can be found in a multitude of tree species (Eberhardt 2000, Lemaître and Villard 2005, Cadieux 2011, Cooke and Hannon 2012, Nappi et al. 2015). The Pileated Woodpecker's foraging excavation densities were associated with a high mean DBH and tree structural diversity. This result corroborates those in other studies for which this woodpecker selected large senescent and dead trees for foraging (Lemaître and Villard 2005, Nappi et al. 2015). For the Yellow-bellied Sapsucker, the density of sapwell trees and its site occupancy was best explained by high tree species diversity which supports its strong selection for mixedwood stands and its ability to create sapwells in multiple tree species (Eberhardt 2000).

Finally, the fact that the best predictor of species richness of deadwood birds was the structural diversity of trees (combining degradation stages and diameter), which reached its highest values in mixedwood stands, pinpoints the importance of old mixedwood forests for deadwood birds. The high diversity of tree size and degradation stages in mixedwood stands provides keystone structures (*sensu* Lindenmayer et al., 2012) for a high number of species associated with deadwood to

satisfy their ecological requirements for both nesting and foraging (Drapeau et al. 2009, Cadieux 2011, Nappi et al. 2015).

1.6.3 Species detection probability

The primary goal of our study was to measure and highlight potential differences in habitat occupancy and use by an assemblage of deadwood associated birds along a composition and structure gradient of forests stands in boreal black spruce landscapes. However, studying this focal group of species can be challenging given the range of variability of individual species' home range sizes. Since this investigation was conducted at the stand level, our study design consisted in a short lasting playback broadcasting (1 minute / species) constrained into a small radius (75 m). While such protocol is adequate for small home range species (chickadees, nuthatches, wrens, small woodpeckers and creepers) it may not be optimal for species with larger home ranges (other woodpeckers). Hence, unsurprisingly we found low detection probabilities for some of our woodpecker species (Pileated, Hairy, Black-Backed, and American Three-toed woodpeckers). Improving the detection probability of these species would require either to conduct a series of playback stations enclosed in a larger sampling unit closer to these species' home range, as was done by Baumgardt et al. (2014), or increase the duration of playback calls to attract species with large territories that will eventually respond to playback (Ibarzabal et Desmeules, 2006). In our study, this limitation of the playback method for detecting large home range species is, however, compensated by our censuses of foraging signs by woodpecker species. In both mixedwood (Pileated and Hairy woodpeckers) and black spruce forests (Black-backed and American three-toed woodpeckers) foraging signs provided critical complementary data on habitat use by these species.

1.6.4 Management implications

Old forests are generally considered important habitats for biodiversity (Spies and Franklin 1996). There is a build-up of species as stands become structurally more

complex with increased diversity of large senescent and decaying trees (Franklin et al. 1987, Newton 1994), creating new habitats for multiple species, of which many are associated with decaying wood (Franklin et al. 1987). In the Clay Belt region of Québec and Ontario, this relationship between old forests and species associated with deadwood is, however, truncated in time by the reduced availability of these structural attributes induced by the process of paludification (Harper et al. 2005, Simard et al. 2007). Hence, the functional role of old-growth boreal forests for deadwood birds is altered by paludification and accordingly, deadwood birds closely track old productive forests. These forests are, however, also prioritized for harvesting since their wood volume is greater. Conventional short rotation even-aged management, which considerably reduces productive old forests and key structural attributes such as old live and dead trees, is thus jeopardizing the conservation of deadwood birds. In forest management units, the inclusion of harvesting practices such as partial cuts and increased variable retention of old forest structural characteristics in clear-cuts (Bergeron et al. 2007, Fenton et al. 2009, Tremblay et al. 2015a), are thus more likely to benefit birds associated with decaying and deadwood in black spruce forests, despite landscapes being marginally or strongly affected by paludification.

While mixedwood stands are rare in northern boreal black spruce forests, our results indicate that they play a pivotal role for deadwood birds and are thus key habitats for this focal group of species. Therefore, the protection of these small and isolated habitats should be a critical component in a conservation strategy of deadwood birds in old forests of the northern boreal black spruce forests.

Finally, increasing our knowledge of habitat occupancy and distribution patterns of deadwood birds in old forests is a first step towards assessing the quality of these habitats for maintaining this focal group of species in the boreal forest. The next step, however, relies on measuring the reproductive activity and success of these birds in

old forests (see Tremblay et al. 2015b). Moreover, determining the ecological interactions of the cavity-nesting community is a promising approach for increasing our understanding of old forests' functional diversity in the boreal ecosystem (Martin et al. 2004, Cockle et al. 2012).

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1.9 Tables

Table 1.1. List and description of habitat variables.

Variable		Description
Composition and Productivity	TreeDiv	Tree species diversity, calculated with the Shannon-Weaver index
	AspenBA	Trembling aspen basal area (m^2/ha)
	BlaSprBA	Black spruce basal area (m^2/ha)
	DBH	Mean diameter of trees at breast height (cm)
	BA	Total tree basal area (m^2/ha)
Quantity and size of deadwood	DdwVo	Downed deadwood volume (m^3/ha)
	DBHdt	Mean diameter of dead trees at breast height (cm) measured for all trees > 10 cm
	RD10-20	Density of recently dead trees (degradation classes 4-5) 10-20 cm DBH per ha
	RD>20	Density of recently dead trees (degradation classes 4-5) > 20 cm DBH per ha
	HD10-20	Density of highly degraded trees (degradation class 6-7-8) 10-20 cm DBH per ha
	HD>20	Density of highly degraded trees (degradation class 6-7-8) > 20 cm DBH per ha
	QuaExc	Density of trees adequate for cavity excavation; trees > 20 cm DBH with degradation class 4-5-6-7-8 or with fungal conks
Tree structural diversity	StrDiv	Tree structural diversity, calculated with the Shannon-Weaver diversity index on degradation and DBH classes

Table 1.2. Comparison between estimates [95% CI] of habitat variables among habitat types. Multi-model inferences on group differences were calculated to identify the habitat types that are significantly different (different letter combinations).

Habitat variables	Black spruce (60-90 years)	Black spruce (90-120 years)	Black spruce (120-160 years)	Black spruce (160-215 years)	Undergoing paludification	Paludified	Mixedwood (70-90 years)	Mixedwood (>90 years)	AICc model selection and Kruskal-Wallis results
TreeDiv	0.20 [0.02, 0.37] **(a)**	0.29 [0.14, 0.44] **(a)**	0.24 [0.10, 0.37] **(a)**	0.23 [0.08, 0.39] **(a)**	0.25 [0.06, 0.43] **(a)**	0.16 [0.02, 0.29] **(a)**	1.45 [1.3, 1.6] **(b)**	1.37 [1.22, 1.52] **(b)**	w_i =1, null model's ΔAIC_c = 131.25
AspenBA (m^2/ha)	0.71 **(a)**	1.27 **(a)**	1.25 **(a)**	0.0 **(a)**	0.0 **(a)**	0.0 **(a)**	13.01 **(b)**	14.40 **(b)**	χ^2_7 = 69.89, P < 0.001
BlaSprBA (m^2/ha)	19.73 [15.63, 23.84] **(c)**	16.93 [13.43, 20.43] **(c)**	14.42 [11.32, 17.52] **(c)**	15.73 [12.06, 19.4] **(c)**	11.54 [7.15, 15.92] **(bc)**	1.33 [0, 4.43] **(a)**	6.53 [3.03, 10.03] **(ab)**	5.97 [2.47, 9.47] **(ab)**	w_i =1, null model's ΔAIC_c = 50.32
DBH (cm)	13.56 [12.44, 14.69] **(b)**	14.6 [13.64, 15.57] **(b)**	14.23 [13.38, 15.09] **(b)**	14.23 [13.22, 15.24] **(b)**	12.77 [11.56, 13.97] **(ab)**	11.36 [10.5, 12.21] **(a)**	18.92 [17.96, 19.88] **(d)**	21.33 [20.36, 22.29] **(e)**	w_i =1, null model's ΔAIC_c = 124.79
BA (m^2/ha)	20.83 [16.15, 25.52] **(b)**	19.4 [15.41, 23.4] **(b)**	15.21 [11.66, 18.75] **(b)**	16.35 [12.16, 20.54] **(b)**	12.47 [7.46, 17.48] **(b)**	1.47 [0, 5.02] **(a)**	32.13 [28.14, 36.13] **(c)**	36 [32, 39.99] **(c)**	w_i =1, null model's ΔAIC_c = 98.48
DdwVo (m^3/ha)	0.04 [0.01, 0.08] **(ab)**	0.11 [0.05, 0.21] **(bcd)**	0.12 [0.07, 0.22] **(bcd)**	0.2 [0.1, 0.39] **(cd)**	0.05 [0.02, 0.13] **(bc)**	0 [0, 0.02] **(a)**	0.36 [0.19, 0.66] **(de)**	1.01 [0.54, 1.88] **(e)**	w_i =1, null model's ΔAIC_c = 68.24
DBHdt (cm)	13.18 [11.93, 14.55] **(bc)**	15.13 [13.9, 16.47] **(cd)**	14.13 [13.11, 15.23] **(bc)**	14.68 [13.43, 16.05] **(bcd)**	12.21 [10.98, 13.58] **(ab)**	10.78 [10, 11.62] **(a)**	17.33 [15.93, 18.86] **(d)**	25.18 [23.14, 27.39] **(e)**	w_i =1, null model's ΔAIC_c = 107.99
RD10-20 (trees/ha)	36.39 [20.03, 66.11] **(ab)**	59.35 [37.3, 93.32] **(b)**	37.38 [23.92, 58.42] **(ab)**	49.27 [30.39, 79.45] **(ab)**	25.5 [11.62, 55.65] **(ab)**	11.92 [4.3, 30.06] **(a)**	40.63 [24.99, 65.97] **(ab)**	24.78 [12.97, 47.01] **(ab)**	w_i = 1, null model's ΔAIC_c = 59.36
RD>20 (trees/ha)	3.13 [0.78, 12.55] **(ab)**	10.61 [5.57, 20.19] **(bc)**	4.76 [2.03, 11.16] **(ab)**	3.33 [1, 11.11] **(ab)**	0 **(a)**	0 **(a)**	12.88 [7.18, 23.1] **(bc)**	28.03 [18.87, 41.64] **(c)**	w_i = 1, null model's ΔAIC_c = 79.22
HD10-20 (trees/ha)	39.58 [21.27, 73.68]	49.24 [30.62, 79.19]	69.64 [48.87, 99.23]	75 [50.08, 112.3]	47.62 [25.99,	14.88 [6.92, 32.02]	90.91 [64.08,	26.67 [13.55, 52.49]	w_i = 1, null model's ΔAIC_c = 101.31

	(acb)	**(acb)**	**(cb)**	**(bc)**	87.25] **(acb)**	**(a)**	128.97] **(c)**	**(ab)**	
HD>20 (trees/ha)	3.12 [0.58, 16.79] **(ab)**	12.88 [6.36, 26.1] **(bc)**	4.76 [1.7, 13.33] **(ab)**	12.5 [5.89, 26.51] **(abc)**	2.38 [0.3, 18.66] **(ab)**	0 **(a)**	30.3 [19.12, 48.02] **(c)**	68.94 [50.8, 93.55] **(d)**	$w_i = 1$, null model's $\Delta AIC_c = 227.05$
QuaExc (trees/ha)	4.17 [0.97, 17.94] **(ab)**	18.94 [10.56, 33.96] **(bc)**	8.33 [3.82, 18.19] **(ab)**	11.67 [5.35, 25.46] **(ab)**	0 **(a)**	0 **(a)**	40.91 [27.49, 60.87] **(c)**	93.18 [71.61, 121.25] **(d)**	$w_i = 1$, null model's $\Delta AIC_c = 326.4$
StDiv	1.02 [0.65, 1.4] **(ab)**	1.6 [1.28, 1.92] **(bc)**	1.64 [1.35, 1.92] **(bc)**	1.8 [1.47, 2.14] **(c)**	1.12 [0.72, 1.52] **(abc)**	0.56 [0.27, 0.84] **(a)**	2.51 [2.19, 2.83] **(d)**	2.77 [2.45, 3.09] **(d)**	$w_i = 1$, null model's $\Delta AIC_c = 75.55$

TreeDiv = Tree composition diversity, AspenBA = Aspen basal area, BlaSprBA = Black spruce basal area, DBH =Mean diameter at breast height, BA = Total tree basal area, DdwVo = Downed deadwood volume, DBHdt = Mean diameter at breast height of dead trees, RD10-20 = Densities of recently dead trees having a DBH of 10-20 cm, RD>20 = Densities of recently dead trees having a DBH > 20 cm, HD10-20 = Densities of highly degraded trees having a DBH of 10-20 cm, HD>20 = Densities of highly degraded trees having a DBH > 20 cm, QuaExc = Densities of trees adequate for cavity excavation, StDiv = Tree structural diversity (see Table 1)

Table 1.3. Observed occurrences, detection probabilities and occupancy probabilities for deadwood bird species measured with the response to playback calls. Values for the observed occurrence are the proportion of sites where there was at least one response to the playback calls in 3 visits. Values for the detection and occurrence probabilities are taken from the null model.

Species	Observed occurrence	Detection probability [95% CI]	Occupancy probability [95% CI]
Yellow-bellied Sapsucker	0.23	0.53 [0.39, 0.67]	0.30 [0.20, 0.42]
Downy Woodpecker	0.09	0.35 [0.15, 0.61]	0.15 [0.07, 0.29]
Hairy Woodpecker	0.11	0.09 [0.01, 0.40]	0.54 [0.03, 0.98]
American Three-toed Woodpecker	0.14	0.13 [0.03, 0.38]	0.47 [0.09, 0.89]
Black-backed Woodpecker	0.14	0.05 [0.03, 0.09]	0.99 [0, 1]
Northern Flicker	0.15	0.18 [0.06, 0.41]	0.39 [0.13, 0.74]
Pileated Woodpecker	0.04	--[a]	--[a]
Boreal Chickadee	0.23	0.12 [0.04, 0.30]	0.84 [0.01, 1]
Red-breasted Nuthatch	0.30	0.38 [0.26, 0.52]	0.46 [0.31, 0.62]
Brown Creeper	0.25	0.24 [0.12, 0.41]	0.52 [0.26, 0.78]
Winter Wren	0.36	0.43 [0.32, 0.55]	0.51 [0.37, 0.66]

[a] Null model did not converge.

Table 1.4. Most-supported models based on Akaike's Information Criterion corrected for small samples (AIC_c) for estimating individual species occurrence in relation to habitat and detection variables. The most supported models ($\Delta AIC_c < 2$) are contrasted to the null model (constant detection and constant occurrence). β values in bold have 95% CI that do not include the zero. Species with a detection probability < 0.15 were not considered (Table 3).

	Model selection					Model estimates / model averaged estimates	
Species	Models	K	AIC_c	ΔAIC_c	w_i	Variable	β [95% CI]
Yellow-bellied Sapsucker	TreeDiv	3	148.96	0.00	0.91	TreeDiv	**2.35 [1.16, 3.56]**
	Null	2	193.32	44.36	0.00		
Downy Woodpecker	DdwVo	3	81.24	0.00	0.27	DdwVo	**1.55 [0.20, 2.90]**
	DBH	4	81.28	0.04	0.27	DBH	**2.22 [0.19, 4.32]**
	BA	3	82.08	0.84	0.18	BA	2.12 [-0.50, 4.75]
	Null	2	95.37	14.13	0.00		
Northern Flicker	Julian+HD10-20	4	126.12	0.00	0.27	HD10-20	1.37 [-0.92, 3.65]
	Julian	3	127.80	1.68	0.12	Julian	**-0.05 [-0.10, -0.01]**
	Null	2	132.15	6.02	0.01		
Red-breasted Nuthatch	ExpObs +BA	4	184.85	0.00	0.75	BA	**2.50 [0.79, 4.21]**
	Null	2	229.15	44.31	0.00	ExpObs	**1.92 [1.03, 2.78]**
Brown Creeper[a]	ExpObs +BA	4	190.13	0.00	0.14	BA	1.21 [-2.47, 4.89]
	ExpObs +DBHdt	4	190.49	0.36	0.12	DBHdt	0.96 [-0.60, 2.51]
	ExpObs +DdwVo	4	190.74	0.60	0.11	DdwVo	0.78 [-0.94, 2.49]
	ExpObs +BlaSprBA	4	190.86	0.72	0.10	BlaSprBA	0.54 [-0.22, 1.31]
	ExpObs	3	191.03	0.89	0.09	ExpObs	**1.01 [0.09, 1.94]**
	Null	2	193.86	3.73	0.02		
Winter Wren	ExpObs + DdwVo	4	241.25	0.00	0.21	DdwVo	**1.74 [0.14, 3.34]**
	Minutes + DdwVo	4	241.86	0.61	0.19	ExpObs	**1.27 [0.47, 2.07]**
	Null	2	259.88	18.63	0	Minutes	**-0.006 [-0.01, -0.002]**

[a] To limit the number of results presented, only the first five models plus the null models are presented as none of the habitat variables were statistically significant.

TreeDiv = Tree composition diversity, BlaSprBA = Black spruce basal area, DBH = Mean diameter at breast height, BA = Total tree basal area, DdwVo = Downed Deadwood volume, DBHdt = Mean diameter at breast height of dead trees, HD10-20 = Densities of highly degraded trees having a DBH of 10-20 cm, StDiv = Tree structural diversity (see Table 1 for more details)

Table 1.5. Most-supported models based on quasi-likelihood Akaike's Information Criterion corrected for small samples ($QAIC_c$) for estimating foraging sign abundances in relation to habitat variables. The most supported models ($\Delta QAIC_c < 2$) are contrasted to the null model. β values in bold have 95% CI that do not include the zero.

Foraging signs	Models	β [95% CI]	K	$QAIC_c$	$\Delta QAIC_c$	w_i
Picoides bark scaling	RD10_20	**0.43 [0.2, 0.65]**	3	105.91	0.00	0.94
	Null		2	121.33	26.12	0.00
Picoides foraging excavations	StDiv	**0.92 [0.68, 1.16]**	3	170.77	0.00	0.99
	Null		2	240.22	69.45	0.00
Pileated Woodpecker's foraging excavations	DBH	**1.36 [0.91, 1.81]**	3	33.44	0.00	0.45
	StDiv	**2.73 [1.52, 3.95]**	3	33.68	0.24	0.40
	Null		2	49.92	16.49	0.00
Yellow-bellied Sapsucker's sapwells	TreeDiv	**1.87 [1.21, 2.53]**	3	35.37	0.00	0.99
	Null		2	61.6	26.22	0.00

StDiv = Tree structural diversity, RD10-20 = Densities of recently dead trees having a DBH of 10-20 cm, DBH = Mean diameter at breast height, TreeDiv = Tree composition diversity

1.10 Figures

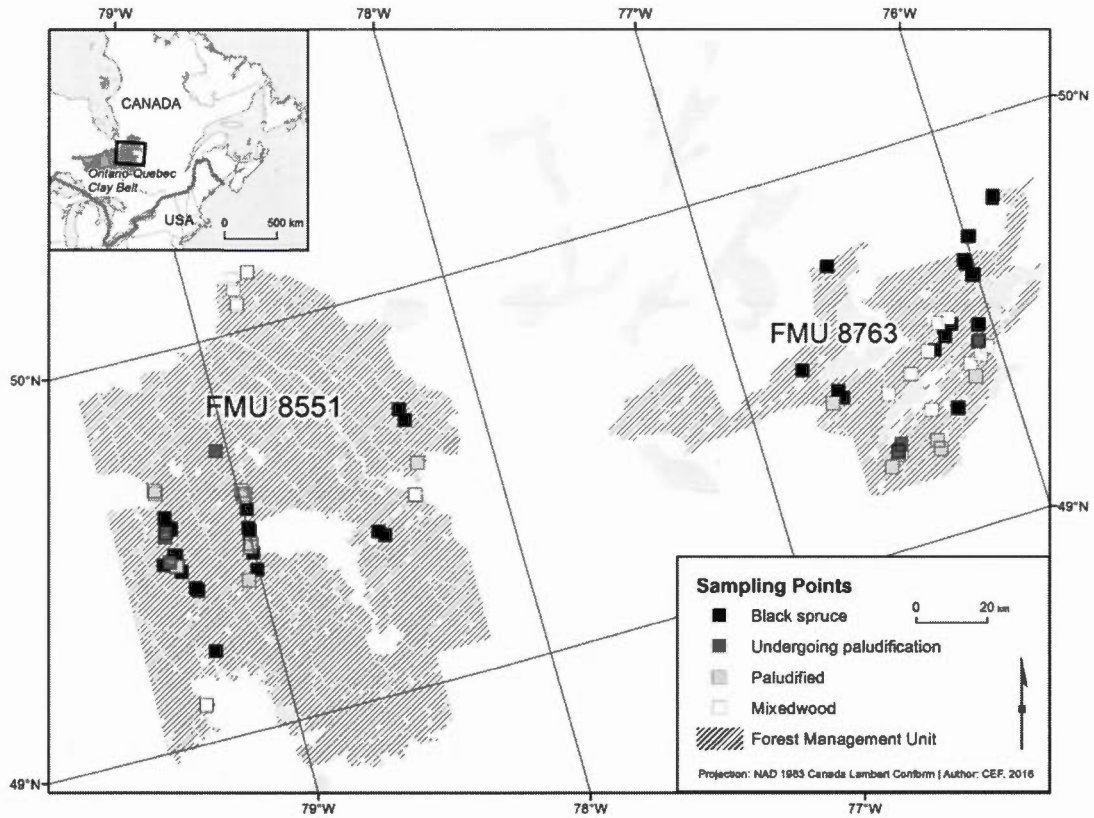

Figure 1.1. Location of sampling sites by forest cover type in northwestern Québec, Canada.

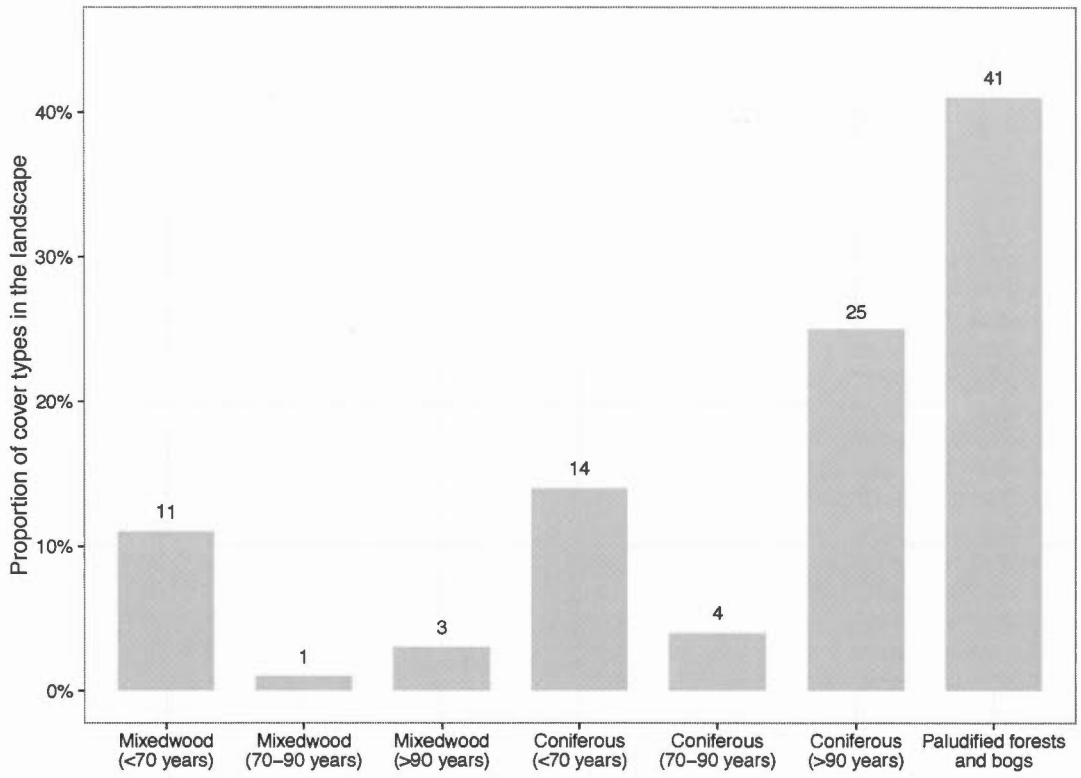

Figure 1.2. Proportion of forest cover types in the studied landscape in northwestern Québec. Proportions are calculated according to categories of forest cover types and age classes available on the digital forest cover maps (MRNF 2011).

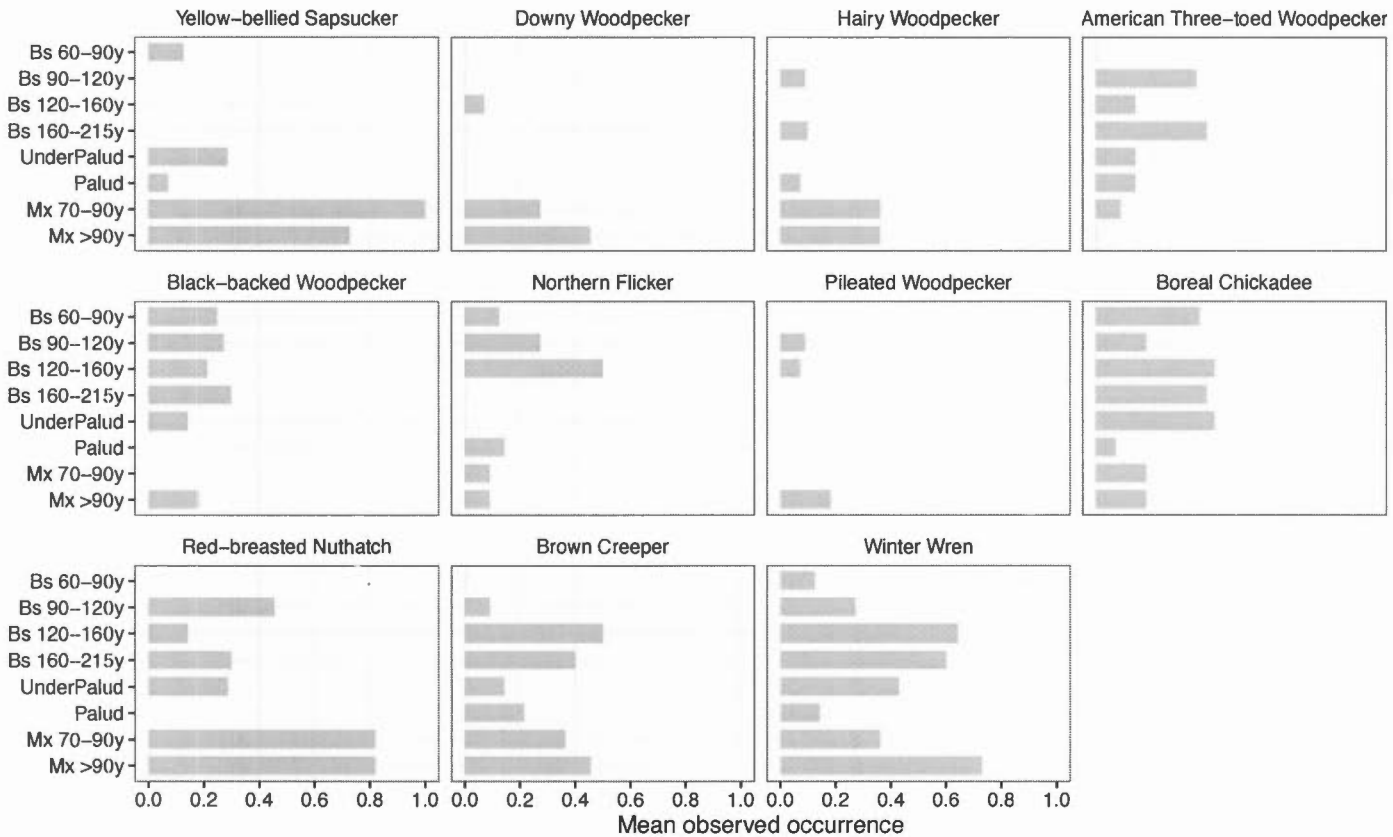

Figure 1.3. Mean observed occurrence per habitat type defined by age and tree species composition in northwestern Québec, Canada. Values for the observed occurrence are the proportion of sites where there was at least one response to the playback calls in 3 visits. Bs = Black spruce, UnderPalud = Undergoing paludification, Palud = Paludified, Mx is for mixedwood.

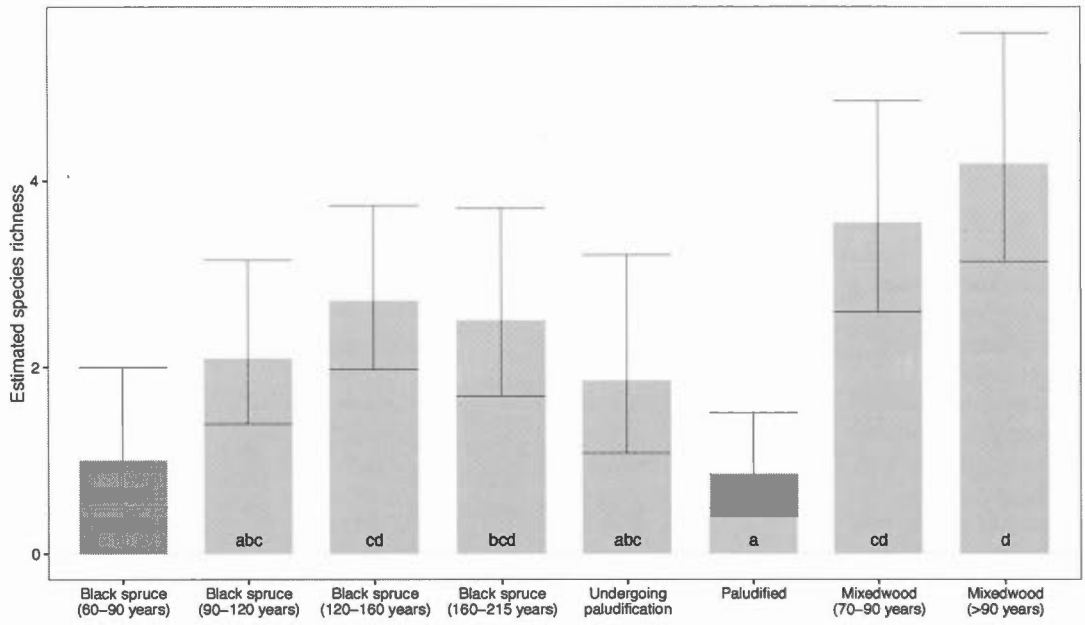

Figure 1.4. Estimated species richness for deadwood birds within 8 habitat types along an age, structure and composition gradient of boreal forests in northwestern Québec. Multi-model inferences on group differences were calculated to identify the habitat types that are significantly different (different letter combinations). The error bars represent the 95% confidence intervals.

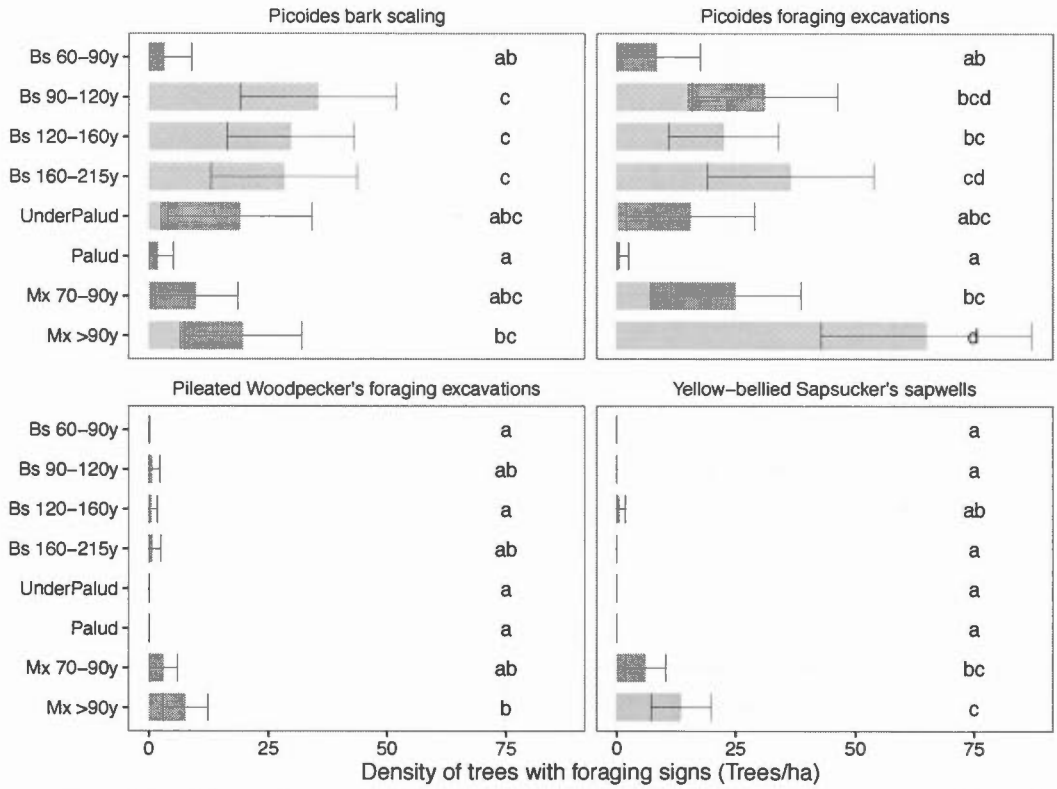

Figure 1.5. Densities of trees with foraging signs for the *Picoides* bark scaling, the *Picoides* foraging excavations, the Pileated Woodpecker's foraging excavations and the Yellow-bellied Sapsucker's sapwells across habitat types. Multi-model inferences on group differences were calculated to identify the habitat types that are significantly different (different letter combinations). The error bars represent the 95% confidence intervals. Bs = Black spruce, UnderPalud = Undergoing paludification, Palud = Paludified, Mx = mixedwood.

1.11 Appendix A.

Table 1A. Species nesting and foraging requirements and association with decaying wood.

Species	Nesting decayed wood association	Foraging decayed wood association and foraging techniques
Yellow-bellied Sapsucker	Excavates nesting cavities in live but senescent or dead large trees[a] (> 95 % of nests in trembling aspen[b])	Forages on live trees Creates sapwells on live deciduous or coniferous trees[c]
Downy Woodpecker	Excavates nesting cavities in large dead trees (> 95 % in trembling aspen[b])	Forages on live and dead trees[c]
Hairy Woodpecker	Excavates nesting cavities in live but senescent or dead large trees[a] (> 80 % in trembling aspen[b])	Forages on dead trees and excavates holes for insects Selects large deciduous dead trees[c]
American Three-toed Woodpecker	Excavates nesting cavities, mostly in coniferous trees	Creates sap wells on live coniferous trees and forages on recently dead trees by scaling bark for bark beetles[cd].
Black-backed Woodpecker	Excavates nesting cavities, mostly in coniferous trees	Forages on dead trees, excavates holes and scales bark for wood-boring beetles[c]
Northern Flicker	Excavates nesting cavities in large dead trees[a] (> 50 % in trembling aspen[b])	Forages mostly on the ground for ants
Pileated Woodpecker	Excavates nesting cavities in large dead trees (> 95 % in trembling aspen[b])	Forages on dead and live trees, excavates big holes for carpenter ants[c]
Boreal Chickadee	Excavates nesting cavities or reuses natural or excavated cavities	Foliage gleaner
Red-breasted Nuthatch	Excavates nesting cavities or reuses natural or excavated cavities in highly decayed trees (> 80 % in trembling aspen[b])	May forage on dead trees
Brown Creeper	Nests in dead trees under raised bark	May forage on dead trees
Winter Wren	May reuse natural or excavated cavities or nests in a cavity in the overturned roots of a fallen tree	Forages on the ground, may forage among fallen trees

[a] >30 cm^2
[b] Regional data (Cadieux 2011)
[c] Regional data (Nappi et al. 2015)
[d] Regional data (Gagné et al. 2007)

CHAPITRE 2

PERSISTENCE, CHANGES AND ROBUSTNESS IN ECOLOGICAL NETWORKS AT THE TRANSITION BETWEEN MIXEDWOOD AND CONIFEROUS BOREAL FORESTS: THE CASE OF NEST WEBS

2.1 Résumé

Les réseaux d'utilisateurs de cavités de l'Amérique du Nord sont composés d'une faible proportion d'espèces ayant beaucoup de liens. Ceci suggère une faible robustesse à la perte d'espèces clés de voûte. Dans l'est du Canada, d'importants changements latitudinaux surviennent dans la structure et la composition forestière partant des forêts boréales mixtes aux forêts boréales résineuses. À cette transition, de vieux arbres décidus de grande taille, soit les arbres principalement utilisés par la faune cavicole, laissent place à de petits arbres résineux, majoritairement l'épinette noire (*Picea mariana*). Nous avons comparé la structure et la robustesse des réseaux d'utilisateurs de cavités de la région de la forêt boréale mixte (48 – 49^{0}N) à la région de la pessière à mousses (> 49^{0}N). Les données ont été récoltées à l'échelle régionale (12 000 km^2) le long d'un gradient latitudinal à la transition entre les forêts mixtes et résineuses dans des forêts à canopée fermée et dans des habitats forestiers ouverts et ennoyés par l'activité du castor (*Castor canadensis*). La structure des réseaux est restée similaire entre la région de la forêt boréale mixte et la région de la pessière à mousses. Premièrement, le rôle clé du peuplier faux-tremble (*Populus tremuloides*) a persisté dans la région de la pessière à mousses malgré l'importance marginale de cette essence d'arbre. Deuxièmement, l'ennoiement des peuplements forestiers par l'activité du castor a hébergé des réseaux riches et complexes dans les deux régions. Dans les deux régions forestières, le Grand Pic (*Dryocopus pileatus*) est demeuré l'espèce pivot pour les espèces d'utilisateurs secondaires de cavités de grande taille en forêts à canopée fermée dominées par le peuplier faux-tremble. Il était, par contre, absent des forêts résineuses à canopée fermée. Le Pic flamboyant (*Colaptes auratus*) est devenu le principal pourvoyeur de cavités de taille moyenne et grande dans ces forêts et par conséquent dans toute la région de la pessière à mousses. Dans les forêts ennoyées des deux régions, le Pic flamboyant était encore le pourvoyeur principal de cavités de taille moyenne et grande. Les réseaux dans les forêts d'épinettes noires étaient beaucoup plus pauvres que ceux dans les vieilles forêts mixtes avec moins d'excavateurs et d'utilisateurs secondaires et avec une quantité limitée de liens et d'interactions. Des analyses de retraits ciblés d'espèces démontrent que les réseaux des forêts à canopée fermée, particulièrement celles des vieilles forêts mixtes, ont une faible robustesse au retrait du peuplier faux-tremble et à moindre degré à la perte du Grand Pic, la majorité des liens étant reliés à ces espèces. Les réseaux d'utilisateurs de cavités des forêts ennoyées par le castor étaient plus robustes principalement à cause de l'utilisation plus diversifiée des essences par les excavateurs. Nous proposons que les cibles prioritaires pour la conservation des espèces cavicoles des forêts boréales doivent inclure (1) la protection des vieilles forêts mixtes avec peuplier faux-tremble et les forêts ennoyées par le castor et (2) le déploiement dans les forêts résineuses productives aménagées d'approches de rétention de parcelles de forêts fermées pourvues d'arbres vivants et morts de gros diamètre.

2.2 Abstract

In eastern Canada, a decline in avian diversity is associated with an important latitudinal shift in forest composition and structure, which occurs from mixedwood to coniferous boreal forest regions. At this transition, large old deciduous trees, the main cavity trees of nest webs, give way to smaller conifer trees, primarily black spruce (*Picea mariana*). We hypothesized that this latitudinal gradient would bring important changes in the functional diversity of ecological networks of vertebrate cavity users (nest webs) as these are composed of a few highly connected species suggesting low system robustness to the loss of keystone species. We compared the structure and robustness of nest webs in balsam fir-white birch (BFWB) and black spruce-moss (BSM) bioclimatic domains. Data was collected at a regional scale (12 000 km^2) along a 200 km latitudinal gradient (48^0-50^0N) at the transition between mixedwood and black spruce dominated regions in old closed-canopy and open forest habitats flooded by the American beaver (*Castor canadensis*). Network structure was surprisingly similar between BFWB and BSM regions. First, the keystone role of old trembling aspen (*Populus tremuloides*) stands persisted in the northern BSM region despite their marginal importance. Second, the flooding of forest stands by beaver ponds harbored similarly rich and complex nest webs in both forest regions. The Pileated Woodpecker (*Dryocopus pileatus*) remained the pivotal species across the two forest regions for large secondary cavity users in closed-canopy forests dominated by trembling aspen, it was, however, absent in closed-canopy black spruce stands. In these latter forests and in open flooded forests, the Northern Flicker (*Colaptes auratus*) was the main medium to large cavity contributor across the two forest regions. Targeted removal simulations highlighted that closed-canopy forest networks, had a low robustness to the removal of trembling aspen and to a lesser degree to the loss of the Pileated Woodpecker, the majority of links within these networks being tied to these two species. Open forests nest webs, created by beaver ponds, were more robust mainly because primary excavators relied on a higher diversity of tree species. We suggest that conservation priorities for the cavity-nesting and roosting community in the northern boreal forest should include (1) the protection of old mixedwood stands and beaver ponds and (2) the retention of old productive coniferous stands with large live and dead trees in managed coniferous landscapes.

2.3 Introduction

One of the most recognized patterns in ecology is the general decline in species diversity along a latitudinal gradient from the tropics to the poles (Rohde 1992, Begon 1986). Along with this trend, a reduction in functional diversity is also observed (Kerkhoff 2012). This pattern is also noticeable within the largest forest biome of the planet, the boreal forest, as avian diversity declines following the habitat gradient which from the south to the north of the boreal forest, corresponds to the transition from mixedwood to coniferous dominated forests where smaller size black spruce (*Picea mariana*) trees prevail (Gauthier et al. 2000, Drapeau et al. 2003). However, some studies found that remnant mixedwood stands in black spruce landscapes were strongly selected by several organisms (the American Marten (*Martes americana*) and the moose (*Alces alces*) (Crête and Courtois 1997, Cheveau et al. 2013). Hence, the conservation of these old mixedwood stands might also be critical for cavity users, which represent an important proportion of the vertebrate diversity that shapes these complex ecological networks in boreal forests (Darveau and Desrochers 2001, Martin et al. 2004, Cadieux 2011).

In boreal ecosystems, these ecological networks (hereafter called nest webs) have a scale-free structure (sensu Barabási 2009) i.e, where few species are responsible for the majority of links and are thus considered network hubs. In these ecosystems the trembling aspen, the Pileated Woodpecker (*Dryocopus pileatus*) and the Northern Flicker (*Colaptes auratus*) have often been identified as such (Martin et al. 2004, Cadieux 2011, Cooke and Hannon 2011, Simard et al. 2013). Having the most connections in these networks, large old senescent and dead trembling aspen are strongly selected by most boreal woodpeckers for cavity excavation as they require a minimal tree size and a specific decay type (Martin et al. 2004, Cadieux 2011, Blanc and Martin 2012, Ouellet-Lapointe et al. 2012). The preferred decay type is heart rot because it creates a soft interior often surrounded by a hard exterior shell (Jackson

and Jackson 2004, Tozer et al. 2012, Lorenz et al. 2015). Whereas scale-free networks are generally tolerant to the loss of random nodes (species), they usually have low system robustness to targeted species removal (Albert et al. 2000, Cockle et al. 2012, Messier et al. 2013, Simard et al. 2013). Along the latitudinal gradient, the loss of keystone structures (Lindenmayer et al. 2012), for instance, large old senescent and dead trembling aspen, could have an important negative impact on the cavity-nesting community limiting the creation of cavities by woodpeckers. However, some cavity excavators like the Northern Flicker could persist since they use a greater diversity of nesting substrates suggesting a higher tolerance to the loss of these keystone structures (Wiebe and Moore 2008).

Trees adequate for cavity excavation are created in multiple ways in the boreal forest. While fire is often cited as the main disturbance, there are multiple other disturbance agents acting at different spatial and temporal scales, which could facilitate the excavation process: wind, fungi, insects and beaver (Holt 1997, Bergeron and Fenton 2012, Nummi and Kuuluvainen 2013). In this study, we focus more closely on two ecological processes that are common and widespread in the boreal forest and could be responsible for providing adequate trees for cavity excavation: a) the senescence of forest stands; b) the flooding of forest stands by the American beaver (*Castor canadensis*). Tree senescence combined with abiotic and biotic factors such as heart rot can generate large cavity trees (Franklin et al. 1987, Bergeron and Fenton 2012). Such is the case for the trembling aspen which, when it ages and reaches large diameters, is often affected by heartwood decay (*Phellinus tremulae*) while still alive (Basham 1991, Hart and Hart 2001, Jackson and Jackson 2004, Cadieux 2011).

As woodpeckers, the American beaver is considered an ecosystem engineer, creating habitat for multiple species (Naiman et al. 1986, Wright et al. 2002). There have been surprisingly few studies that considered the beaver as an agent of boreal forest dynamics' (Grover and Baldassarre 1995, Rosell et al. 2005, Nummi and

Kuuluvainen 2013) and even less on cavity-nesting bird communities (Lochmiller 1979). Snags in beaver ponds may provide an important source of cavity trees in forest landscapes highly disturbed by beaver activities such as is the case in our study region. Acting like a straw, a flooded tree has its roots and lower trunk most of the time under water whereas the top of the tree is usually in an open environment with direct sunlight, which hardens its exterior. A humid environment favors rapid development of fungi and decay organisms in flooded trees (Jackson and Jackson 2004), facilitating their excavation. Moreover, in a context such as the black spruce-moss forest region, where old large aspens become rare and patchily dispersed across the landscape, beaver ponds could compensate for the limited sources of cavity trees adequate for excavation.

In this study we analyze the structure of nest-webs along a latitudinal gradient from mixedwoods to coniferous boreal forests of eastern Canada. We focus on specific habitats rich in senescent and dead cavity trees in both closed-canopy forests and open forest habitats flooded by the American beaver. We compare the characteristics of cavity trees to available trees, and differences in interactions and species composition in mixedwood, coniferous and beaver ponds stands. We test the robustness of nest webs with a species removal analysis focused on keystone species. We hypothesize that the changes in the availability of adequate cavity trees along our latitudinal gradient will affect the cavity-nesting communities by changes in the structure of networks at the tree and cavity excavator levels. We predict that the strong tree diameter gradient and the changes in tree species composition from mixedwood to coniferous regions will most likely affect large cavity nesters like the Pileated Woodpecker. The functional role of large cavity provider in coniferous boreal landscapes will shift from this excavator to the Northern Flicker, which has been shown to be more flexible in its nesting substrates (Wiebe and Moore 2008). We also predict that nest webs in open forest habitats will be more diversified and rich in the coniferous region than in the mixedwood region given the reduced availability of

adequate cavity trees in black spruce closed-canopy forests and the reduced amount of old mixedwood stands. Hence, nest webs of open forests in the northern coniferous matrix of the boreal forest could compensate for the lower contribution of closed-canopy forest stands (black spruce and mixedwood combined).

2.4 Methods

2.4.1 Study area

Our study spans a ~ 200 km latitudinal gradient from the balsam fir-white birch (BFWB) to the black spruce-moss bioclimatic domain (BSM) located in northwestern Québec in the northern Clay Belt of Quebec and Ontario (Robitaille and Saucier 1998). It covers a study region of 12 000 km^2 (Figure 1). The BFWB region is characterized by clay soils and low rocky hills (Robitaille and Saucier 1998). The area contains a complex natural forest mosaic formed by different forest cover types and by a variety of natural disturbances (Harvey 1999). The BSM has a generally flat topography (Robitaille and Saucier 1998) and is known for its high vulnerability to paludification, a process of gradual conversion of a mesic forest to a forested peatland through the accumulation of organic material and water table rise (Taylor et al. 1988, Simard et al. 2007). The forest mosaic is dominated by black spruce stands (Gauthier et al. 2000).

2.4.2 Sampling plots

Sampling plots were vastly dispersed throughout the landscape to cover at a regional scale the entire study region (Figure 2.1). In the BFWB region, plots were located in the Lake Duparquet Research and Teaching Forest (LDRTF) at the southern fringe of the boreal forest in Québec (48°30' N, 79°22' W) (Figure 2.1). Research on cavity nesters is undergoing since 2003 (Nappi 2009, Cadieux 2011, Nappi et al. 2015). In the BFWB region, we established 12 sampling plots in 2003 (24-40 ha) distributed in four forest age categories (61-89, 135, 182-208 and 245 years after fire) determined

from prior knowledge of the fire regime and fire history over the last three centuries in the LDRTF area (Bergeron 1991, Dansereau and Bergeron 1993). These age categories determined by time since last fire were chosen to represent the structural and compositional changes that occur in the mixedwood forest from early to late successional stages. Stand composition changed with time since fire, from early seral stands dominated by deciduous stands composed of trembling aspen and paper birch (*Betula papyrifera*), to mixed stands incorporating white spruce (*Picea glauca*) and balsam fir (*Abies basamea*), to coniferous stands with balsam fir, white and black spruce and eastern white cedar (*Thuya occidentalis*) (Bergeron 2000). In addition, we established 20 mixed and coniferous plots in beaver ponds of varying size (10 mixedwood ponds and 10 coniferous ponds).

In the BSM region, stand composition of this portion of our study region is dominated by coniferous stands of black spruce of differing stand ages (Gauthier et al. 2000). We established 24 sampling plots (10 ha) in unharvested old forest stands dominated or co-dominated by trembling aspen (12) and by black spruce (12). These plots were selected with updated digital forest cover maps (MRNF 2011). To be selected, a forest patch had to be 1) accessible by road; 2) an old forest (categorized by the digital cover maps to be older than 70 years after fire); 3) large enough to fit a 10 ha plot (250 m by 400 m); and 4) at least 2 km from another sampling plot. Using the same methodology as in the BFWB forest region, 24 plots of varying size were established in beaver ponds (12 in mixedwood ponds and 12 in coniferous ponds).

2.4.3 Nest search and cavity monitoring

In the BSM region, nest searches were conducted between the beginning of May and the middle of July. Observers walked along transects separated by 50 m and used visual and auditory cues that would indicate the presence of an occupied cavity: breeding-bird behavior, begging nestlings or wood chips on the ground. Observers also scanned trees for cavities. When possible, the excavator of the cavity was

visually identified. If no excavator was present at the site, we estimated the excavator with the size and characteristics of the cavity. If there was a doubt, the excavator remained unidentified. Two search surveys were made during the breeding season. The methodology is very similar for the BFWB region and described in Cadieux (2011). In beaver ponds, observers did a first cavity search survey by walking around the pond and spot mapping all cavity-nesting species, potential nests and cavity trees. The second survey was done with high boots and a canoe in which every tree was inspected for cavities. Furthermore, to ensure a regional perspective and to include as many interspecific interactions as possible, we took advantage of the lengthy travel time between plots to opportunistically find occupied cavities along the road network.

All trees with cavities were marked with an aluminum tag and geo-referenced. They were characterized by their essence, diameter at breast height (DBH) and degradation (live or dead) and were also checked for exterior signs of heart rot by noting the presence of fungal conks of fungal species associated to heartwood decay. Cavities were inspected with a camera mounted on a telescopic pole (TreeTop Peeper™, Sandpiper Technologies, Manteca, California) to determine the state of the cavity: non-completed excavation, suitable cavity or occupied cavity. A cavity was considered "occupied" if it contained at least one egg or nestling, or if a mammal was present inside the cavity (Martin et al. 2004).

2.4.4 Vegetation sampling

Vegetation sampling was conducted to characterize and compare cavity trees to available trees. Available trees having a DBH >10 cm were characterized by: tree species, DBH, and tree degradation (live or dead and presence or absence of fungal conks).

In the BFWB region, vegetation sampling was done in rectangular shaped subplots measuring 600 m^2 (10 m X 60 m), which were distributed 200 m apart in each closed-

canopy forest plot. In the BSM region, this sampling was done in 16 variable-area subplots which were placed systematically in the closed-canopy forest plots. Factor 2 prisms were used to select trees. In beaver ponds, since access was difficult, we sampled trees based on their accessibility.

2.4.5 Landscape scale characteristics

Proportions of forest cover types in each forest region were measured with digital forest cover maps (MRNF 2011). Only polygons representing forested land were used to compute the proportion of habitat types by their composition in the landscape.

2.4.6 Statistical analyses

2.4.6.1 Local scale characteristics

Characteristics of cavity trees, and available trees were compared between open and closed-canopy habitats and for the two forest regions by averaging values at the plot. Closed-canopy habitats were split into mixedwood and coniferous forest cover because of striking differences in tree characteristics. We compared the mean DBH as well as the proportion of dead trees, coniferous trees, trembling aspens and trees with fungal conks. The mean DBH was computed for trees > 10 cm in DBH whereas all other tree characteristics were computed for trees of DBH > 20 cm. All mean comparisons were made with a Kruskal-Wallis test since variables were non-normally distributed.

2.4.6.3 Nest-web structure and robustness to the loss of keystone species

To compare species interactions of trees, cavity producers and cavity users along the latitudinal gradient, we built nest webs in the BFWB and BSM regions for both closed and opened canopy forests. For each nest web, we separated the coniferous trees and deciduous trees to highlight interactions between excavators and trees. Strength of interactions is computed for each link between species and was calculated separately for two levels: the tree to excavator level and the cavity reuse level. The

linkage strength for cavity reuse by secondary cavity nesters (SCN), weak primary cavity nesters (WPCN) or primary cavity nesters (PCN) was calculated as the proportion of total nests located in cavities not excavated by the focal species. The linkage strength between a tree species and an excavator was defined as the proportion of an excavator's nests located in a tree species. Three categories of linkage strength were used: weak links (< 10 %), medium links (11-50 %) and strong links (> 50 %) (Martin and Eadie 1999). In order to compute interaction diversity, every occupied cavity was categorized on the basis of its interspecific interactions stemming from three different levels across our networks: the tree level, the excavator level and the secondary cavity nesters level.

Sampling with replacement was used to calculate the means and 95 % confidence intervals of different network characteristics between habitats using 10 000 permutations. We compared Shannon-Weaver's diversity index for tree species, woodpecker species and secondary cavity nesters and interspecific interactions for each resampled network. The sampling size was set to the lowest network size (79 nest trees) in order to equilibrate the number of occupied cavities by habitat. Differences between habitats were considered significant when the confidence intervals did not overlap.

Using the same resampling method, we evaluated the robustness of networks to the loss of specific species. In this case, for each permutation, after having sampled the data, we removed a specific species. We removed excavator species (Downy Woodpecker - *Picoides pubescens* , Yellow-bellied Sapsucker - *Sphyrapicus varius*, Black-backed Woodpecker - *Picoides arcticus* , Northern Flicker or the Pileated Woodpecker) and tree species (trembling aspen, black spruce, balsam fir, white birch, balsam poplar - *Populus balsamifera*). We then measured the proportion of secondary extinctions (loss of other species).

All statistical analyses were performed with R version 3.2.3 (R Core Team 2015) and graphics were created with the R package: ggplot2 (Wickham et al. 2013).

2.5 Results

2.5.1 Landscape scale characteristics of forest regions

In the BSM region, bogs covered 41 % of the landscape in contrast to only 10 % in BFWB (Figure 2.2). Conifer forests older than 70 years were well represented in the BSM with 29 % and 17% in BFWB (Figure 2.2). Only 3 % and 8 % of mixedwood forest cover > 70 years was found in BSM and BFWB regions respectively compared to 8 % and 21 % of mixedwood forests < 70 years for BSM and BFWB respectively (Figure 2.2). A similar trend was observed with deciduous forests with only 1 % and 4 % of forests > 70 years cover found in BSM and BFWB respectively (Figure 2.2).

2.5.2 Local scale characteristics

At the stand scale, we observed different selection patterns between open and closed-canopy forests when cavity trees characteristics were compared to ones of available trees with the exception of tree diameter (DBH). Cavity trees had a significantly higher DBH than available trees in every sampled habitat (Table 2.1). The smallest mean DBH were found in coniferous closed canopy forests for both available and used trees (Table 2.1). There was a significantly higher proportion of dead trees used as cavity trees than for available trees in closed-canopy forests (Table 2.1). In beaver ponds most trees used and available were dead (Table 2.1). Deciduous trees, mostly trembling aspen were strongly selected as cavity trees in closed-canopy forests whereas, in beaver ponds, this was much less the case as this preference for deciduous trees was only significant in beaver ponds of the mixedwood forest region (Table 2.1). Finally, cavity trees in closed canopy forests had a significantly higher proportion of the presence of fungal conks than available trees (Table 2.1). However

this selection was not observed in beaver ponds and to the contrary, cavity trees had a significantly lower proportion of fungal conks than available trees (Table 2.1).

2.5.4 Nest-webs structure and robustness to the loss of key species

During the field seasons of 2012 and 2013 in the BSM region, we found 249 nests and occupied cavities for 20 cavity-nesting species. In the BFWB region, throughout the 2003 to 2015 period, we found 844 nests and occupied cavities for 22 cavity-nesting species. Most cavity nesters found in the BFWB forest region were also found in the BSM region with the exception of the Wood Duck (*Aix sponsa*), the Common Raccoon (*Procyon lotor*) and the Northern Hawk Owl (*Surnia ulula*). Moreover, the American Three-toed Woodpecker (*Picoides dorsalis*) and the Boreal Owl (*Aegolius funerus*), which were absent in the BFWB region, were added in the BSM region cavity-nesting community. Across forest regions only 5 % of nests were found in coniferous trees (n = 56), mostly in black spruce and 95 % of nests were found in deciduous trees, mostly in trembling aspen (n = 1034) (Figure 2.3). Only a few excavators such as the Boreal Chickadee (*Poecile hudsonicus*), the Black-capped Chickadee (*Poecile atricapillus)* and the Northern Flicker were found in both coniferous and deciduous trees. All cavity excavators were found to use deciduous trees at least once for nesting with the exception of the Black-backed Woodpecker.

In BSM's closed-canopy forests, the majority of cavity trees were in deciduous trees. We found only a limited number of cavities in coniferous trees that were mainly excavated by the Black-backed Woodpecker and the Northern Flicker (Figure 2.3b). The BSM's deciduous tree nest web contained a diverse community of cavity nesters very similar to what was observed in the BFWB deciduous tree nest web (Figures 5a,b). In both nest webs, the structure was centered on the trembling aspen as the main nest tree, the Yellow-bellied Sapsucker as the main cavity excavator and nester and around the Pileated Woodpecker, which was the cavity excavator with the most cavities reused by secondary cavity nesters (Figures 5a, b).

The majority of nests in coniferous trees were found in beaver ponds (82 %). In this habitat the Northern Flicker was the main cavity excavator and cavity nester. It also re-excavated (enlarged) and reused existing cavities excavated by the Black-backed Woodpecker and the American Three-toed Woodpecker (Figure 2.3d). Afterwards, secondary cavity nesters reused some of these cavities. Overall, the Northern Flicker was the excavator species having the most re-excavations of all species (Figures 5a, b, c, d). BSM beaver ponds were similar to BFWB beaver ponds. However, the community of cavity nesters also included a higher proportion of species associated to closed-canopy mixedwood forests as some BFWB beaver ponds were surrounded by closed-canopy forests (Figure 2.3c, d). These networks contrasted with those of the BSM as they included cavities excavated by the Pileated Woodpecker and larger secondary cavity nesters. Interestingly, the only other tree species used by the Pileated Woodpecker for cavity excavation was the balsam poplar in a beaver pond (Figure 2.3c). In addition, there were fewer coniferous trees used, probably because of a higher proportion of trees were deciduous even in conifer dominated beaver ponds and these seemed to be preferred (Figure 2.3c).

Nest webs' tree species diversity was highest in beaver ponds and lowest in closed-canopy forests for both forest regions (Figure 2.4). Primary cavity excavators' (Woodpecker) diversity was, however, higher in closed-canopy forests than in beaver ponds (Figure 2.4). But this difference was not significant for BFWB closed-canopy forests. Secondary cavity nesters diversity did not differ significantly between nest webs as all confidence intervals overlapped (Figure 2.4). Interaction diversity was highest in beaver ponds perhaps because of the higher diversity of tree species but BSM closed-canopy nest webs did not differ significantly from the beaver ponds nest webs (Figure 2.4).

In our simulations, the removal of keystone species had important repercussions on the cavity-nesting community. The removal of the Pileated Woodpecker caused a high proportion of secondary extinctions of secondary cavity nesters with a loss ranging from 39 % in BSM forests to 50 % in BFWB forests (Figure 2.5a). The removal of the Northern Flicker had a high impact in beaver ponds reaching 63 % of secondary extinctions in BSM beaver ponds (Figure 2.5a). The removal of other excavating species did not cause a significant effect as most of the confidence intervals included zero (Figure 2.5a). When simulating the removal of tree species in closed-canopy forests, the removal of trembling aspen caused the highest proportion of secondary extinctions reaching 81 % in the BFWB region and 70 % in the BSM forest region (Figure 2.5b). Beaver ponds displayed a higher robustness to the loss of trembling aspen with proportions of secondary extinctions reaching 8 % for BSM beaver ponds and 22 % for BFWB beaver ponds (Figure 2.5b).

2.6 Discussion

To our knowledge, this study is among the first to document and compare at a regional scale, ecological networks of cavity-nesting communities in habitats embedded in contrasted boreal forest matrices. Along our latitudinal gradient ranging from mixedwood to coniferous boreal forests, we observed changes, persistence and robustness in nest webs. The drastic reduction in the availability of large senescent and dead trees adequate for cavity excavation was associated with important changes and losses in the structure of nest webs. But surprisingly, some key elements in these networks persisted throughout the gradient. Networks with higher complexity, represented by interspecific interactions diversity, were more robust to the loss of keystone species. Old trembling aspen forests and beaver ponds were found to be critically important in maintaining complex cavity nesters communities across the latitudinal gradient of forest composition in this part of the Canadian boreal forest.

2.6.1 Stand senescence and beaver flooding at the root of nest webs along the latitudinal gradient

While forest stand senescence was a key driver, notably in mixedwood stands, for the cavity-nesting and roosting community throughout our study region, forest flooding by the beaver was an indisputable key disturbance agent at the root of rich and complex nest webs. These two ecological processes provided adequate cavity excavation trees even though their contribution differed in quality and availability throughout the boreal landscape.

The importance of stand senescence in mixedwood persisted across the latitudinal gradient as it was responsible for the creation of large senescent and dead trees that were at the base of complex nest webs. Old mixedwood stands in the BSM region were used by a diverse community of cavity nesters very similar to the one in the BFWB forest region even though the regional importance of these stands was marginal and our sampling effort spanned over a much shorter time period (2 years vs. 12 years). Occupied cavities were mainly in large senescent or dead trembling aspen infected by heart rot as indicated by the presence of *Phellinus tremulae* fungal conks (Cadieux 2011, Cooke and Hannon 2012). As in other studies in the boreal forest, the nest web structure was centered around decaying and dead trembling aspens, the Yellow-bellied Sapsucker as the main small cavity excavator (its western counterpart being the Red-napped Sapsucker - *Sphyrapicus nuchalis*) and the Pileated Woodpecker which was the excavator of highly reused large cavities (Martin et al. 2004, Cooke and Hannon 2011). This finding reiterates the overwhelming importance of old mixedwoods with trembling aspen for maintaining complex cavity-nesting communities throughout the boreal forest including northern landscapes dominated by coniferous forests. Hence, even in the highly isolated mixedwood forests located in Muskuchii Hills (north of 50°N; Figure 2.1), the network of cavity nesters was very similar to ones located in the southern fringe of boreal forest where aspen stands are

common (Bergeron 2000). However, more research is needed to assess whether habitat quality (measured by reproductive success of cavity nesters) of these isolated forests is as good as southern mixedwood stands.

Along the latitudinal gradient nest webs had low system robustness to the loss of the trembling aspen, a central node in many North American nest webs (Martin et al. 2004, Cadieux 2011, Cooke and Hannon 2011, Cockle et al. 2012, Simard et al. 2013). The removal of this tree species caused important losses in species triggering up to 80 % of secondary extinctions in simulated networks. Correspondingly, numerous woodpecker species nested almost exclusively in mixedwoods and were not found in coniferous dominated habitats. BSM closed-canopy black spruce forests did not foster a complex cavity-nesting community as we found only a limited number of nests and cavity trees. Even though these forests were old (> 90 years), the amount of large and dead trees was low. Black spruce stands in our study were very limited in diameter suggesting low productivity resulting from paludification (Fenton et al. 2005). Further studies on cavity-nesting communities and nest webs in coniferous forests composed by other conifer species and/or with a higher productivity such as those in eastern Québec could either corroborate or provide new insights on the contribution of coniferous forests to nest webs in the black spruce forest region (see Imbeau and Desrochers 2002, Vaillancourt et al. 2008, Tremblay et al. 2009).

In both BSM and BFWB regions, forests flooded by the beaver had rich and diverse cavity user networks. These nest webs had a higher complexity and displayed higher robustness to the loss of the trembling aspen along the gradient. Contrary to closed-canopy forests, these habitats remained highly used regardless of tree species composition and most occupied cavities in coniferous trees in the whole study region were found in beaver ponds. These networks were as rich in the BSM as in the BFWB, thus our hypothesis of higher network complexity in the BSM was not

supported. However, their relative importance was higher in these coniferous landscapes. Where large dead trees were not common, forests flooded by the beaver provided a rare resource of trees adequate for excavation readily used by cavity nesters. The cavity-nesting community occupying this habitat was composed mainly of open forest habitat species with the Northern Flicker as the main cavity excavator and the species with the highest number of occupied cavities. The low mean cavity height in forests flooded by the beaver did not seem to deter the use of cavities (Appendix B). Water might thus act as protection for cavity users. More research on nesting success of cavity-nesting birds in beaver ponds could determine if predation risk is indeed reduced in this habitat. Although beaver ponds are known to be species rich (Wright et al. 2002), there are only a few studies that highlight their importance for dead wood associated birds (Lochmiller 1979, Rendell and Robertson 1989, Grover and Baldassarre 1995, Nummi and Holopainen 2014). To our knowledge this is the first study that measures the importance of forests flooded by the beaver in boreal forest for cavity-nesting communities.

It is noteworthy to mention that more nests of Black-backed Woodpeckers were found in forests flooded by beavers than in closed-canopy forests. Our results may not be surprising considering that in the eastern boreal forest of Canada, 1) Black-backed Woodpeckers reach their highest nesting densities in open habitats originating from recent wildfires (Nappi et al. 2003, Nappi and Drapeau 2009, Nappi et al. 2010), 2) are much more dispersed in old black spruce forests, with large home range and low breeding densities, and 3) are often nesting in remnant snags of recent clearcuts (Tremblay et al. 2009, 2015).

2.6.2 Keystone excavators along the latitudinal gradient

The Pileated Woodpecker was a keystone species for providing high, large and greatly reused cavities to the most and to the largest of secondary cavity nesters, similar to what was found in other studies (Bonar 2000, Aubry and Raley 2002,

Martin et al. 2004, Blanc and Walters 2008, Cooke 2009, Cadieux 2011). However, we confirmed this role throughout our latitudinal gradient as this excavator was as important in BFWB mixedwood stands as it was in BSM mixedwoods. The loss of this keystone species in coniferous dominated forests along the latitudinal gradient and in targeted removal simulations had a strong negative impact on the species diversity of secondary cavity nesters. Large secondary cavity users who nested almost exclusively in its cavities were severely limited. Other studies also found that the distribution of the Pileated Woodpecker was strongly limited by the amount of mixedwood and trembling aspen stands in eastern Quebec boreal forest at slightly lower latitudes (Savignac et al. 2000, Gagné 2006, Vaillancourt et al. 2009).

The Northern Flicker, the second-largest cavity excavator of North American boreal forests, was not limited by the presence of trembling aspen. As found in the literature (Wiebe and Moore 2008), this species was flexible in its tree species selection for cavity excavation. This flexibility was probably one of the reasons why medium to large cavities persisted in boreal coniferous landscapes. The Northern Flicker cavities were still common in open and closed-canopy forests where the trembling aspen was absent. Hence, several cavity nesters of different sizes used northern flicker cavities. One of the largest cavity nesters, the Common Goldeneye was found nesting in a cavity excavated by this excavator in a black spruce in one of our beaver pond sites, showing that this large secondary cavity nester can use the Northern Flicker cavities. With time, cavities originating from Northern Flicker excavations can become bigger (Edworthy et al. 2012) and be used by larger secondary cavity nesters. However, compared to the Pileated Woodpecker cavities which are typically excavated in live but senescent trees in boreal forests making them persistent in time, holes excavated by the Northern Flicker are usually not the ideal choice since excavated trees are usually smaller in diameter, dead and cavities are usually lower making them less secure and ultimately more prone to predation (Fisher and Wiebe 2006). However, these may be the only possible choice for large cavities users in coniferous boreal

forests since cavities excavated by Pileated Woodpecker or created by decay alone, are extremely rare (this study and Vaillancourt et al. 2009). The combination of two ecosystem engineers, the beaver and the Northern Flicker might provide the last large nesting cavity option as we move up north in boreal coniferous landscapes. Our results corroborate Robles and Martin's (2014) idea that habitat may mediate the interspecific associations between cavity excavators and secondary cavity users. In boreal black spruce dominated landscapes where trembling aspen is rare, the key role of large cavity provider thus shifts towards the Northern Flicker.

2.6.3 Protection of old trembling aspen patches and management of productive old coniferous forests

Numerous cavity nesters species were only found in mixedwood stands. For these species, old mixedwood forests with senescent trembling aspen in the BSM region most likely trace their northern distribution limit. Whereas mixedwood forests were very similar in the two regions, BSM mixedwoods represented only 4 % of the forest cover in the landscape. To this day, these forests stands are managed without considering their overwhelming importance for the maintenance of species richness, conservation of biodiversity in general (Jacqmain et al. 2008, Cheveau et al. 2013). Our study clearly reiterates the ecological importance of protecting mixedwood patches in the northern boreal forest considering their regional contribution for the cavity user community.

In northwestern Quebec, old growth black spruce forests often have a very low productivity caused by paludification (Boudreault et al. 2002, Fenton et al. 2005). Cavity nesters are highly dependent on the size of trees. To maintain complex cavity-nesting and roosting communities in a coniferous boreal landscape it is therefore crucial to increase the amount of large live and dead trees in managed landscapes with a mixture of management approaches that may include extensive use of longer rotations, partial cutting, or a combination of both (Bergeron et al. 2002, Gauthier et

al. 2009). These management approaches are not only more likely to be ecologically sustainable for boreal birds (Drapeau et al. 2016) but also for key ecological processes (large tree production and recruitment of deadwood) underlying the complex ecological networks that support cavity-nesting and roosting communities in the boreal forest.

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2.8 References

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2.9 Tables

Table 2.1. Comparisons of average proportions (± SD) of cavity trees and available trees characteristics. Characteristics were compared between cavity trees and available trees, for each habitat types in the two forest regions (BFWB = balsam fir-white birch region , BSM = black spruce-moss region) with Kruskal-Wallis tests.

		BFWB region				BSM region					
Variables		Mixedwood	χ^2 and *P*-value	Beaver ponds	χ^2 and *P*-value	Mixedwood	χ^2 and *P*-value	Coniferous	χ^2 and *P*-value	Beaver ponds	χ^2 and *P*-value
Mean DBH of trees	Cavity trees	37.0 ±4.5	$\chi^2 = 17.28$, $P < 0.001$	33.0 ±12.0	$\chi^2 = 21.41$, $P < 0.001$	32.8 ±6.1	$\chi^2_1 = 12.81$, $P < 0.001$	25.6 ±9.6	$\chi^2 = 12.79$, $P < 0.001$	28.3 ±8.0	$\chi^2 = 16.57$, $P < 0.001$
	Available trees	18.1 ±1.7		20.1 ±3.7		17.3 ±2.3		14.1 ±0.7		17.0 ±3.7	
Proportion of dead trees	Cavity trees	0.44 ±0.09	$\chi^2 = 15.87$, $P < 0.001$	1.00 ±0.00	$\chi^2 = 1$, $P = 0.32$	0.62 ±0.19	$\chi^2 = 12.82$, $P < 0.001$	0.95 ±0.10	$\chi^2 = 13.58$, $P < 0.001$	1.00 ±0.01	$\chi^2 = 2.06$, $P = 0.15$
	Available trees	0.23 ±0.06		0.98 ±0.08		0.21 ±0.12		0.18 ±0.09		0.98 ±0.05	
Proportion of Coniferous trees	Cavity trees	0.00 ±0.01	$\chi^2 = 19.11$, $P < 0.001$	0.27 ±0.44	$\chi^2 = 7.58$, $P = 0.006$	0.00 ±0.00	$\chi^2 = 18.02$, $P < 0.001$	0.77 ±0.37	$\chi^2 = 0.02$, $P = 0.88$	0.68 ±0.36	$\chi^2 = 5.00$, $P = 0.03$
	Available trees	0.41 ±0.20		0.56 ±0.33		0.37 ±0.16		0.91 ±0.16		0.44 ±0.44	
Proportion of trembling aspen	Cavity trees	0.91 ±0.12	$\chi^2 = 16.45$ $P < 0.001$	0.33 ±0.48	$\chi^2 = 0.48$ $P = 0.49$	0.98 ±0.04	$\chi^2 = 16.93$ $P < 0.001$	0.16 ±0.34	$\chi^2 = 0.56$ $P = 0.46$	0.16 ±0.06	$\chi^2 = 1.64$ $P = 0.20$
	Available trees	0.31 ±0.20		0.18 ±0.28		0.60 ±0.17		0.01 ±0.02		0.04 ±0.05	
Proportion of trees with fungal conks	Cavity trees	0.87 ±0.08	— [a]	0.09 ±0.22	$\chi^2 = 16.81$ $P < 0.001$	0.68 ±0.21	$\chi^2 = 15.79$ $P < 0.001$	0.10 ±0.20	$\chi^2 = 2.14$ $P = 0.14$	0.13 ±0.22	$\chi^2 = 11.00$ $P < 0.001$
	Available trees	— [a]		0.42 ±0.25		0.18 ±0.06		0.09 ±0.09		0.45 ±0.34	

2.10 Figures

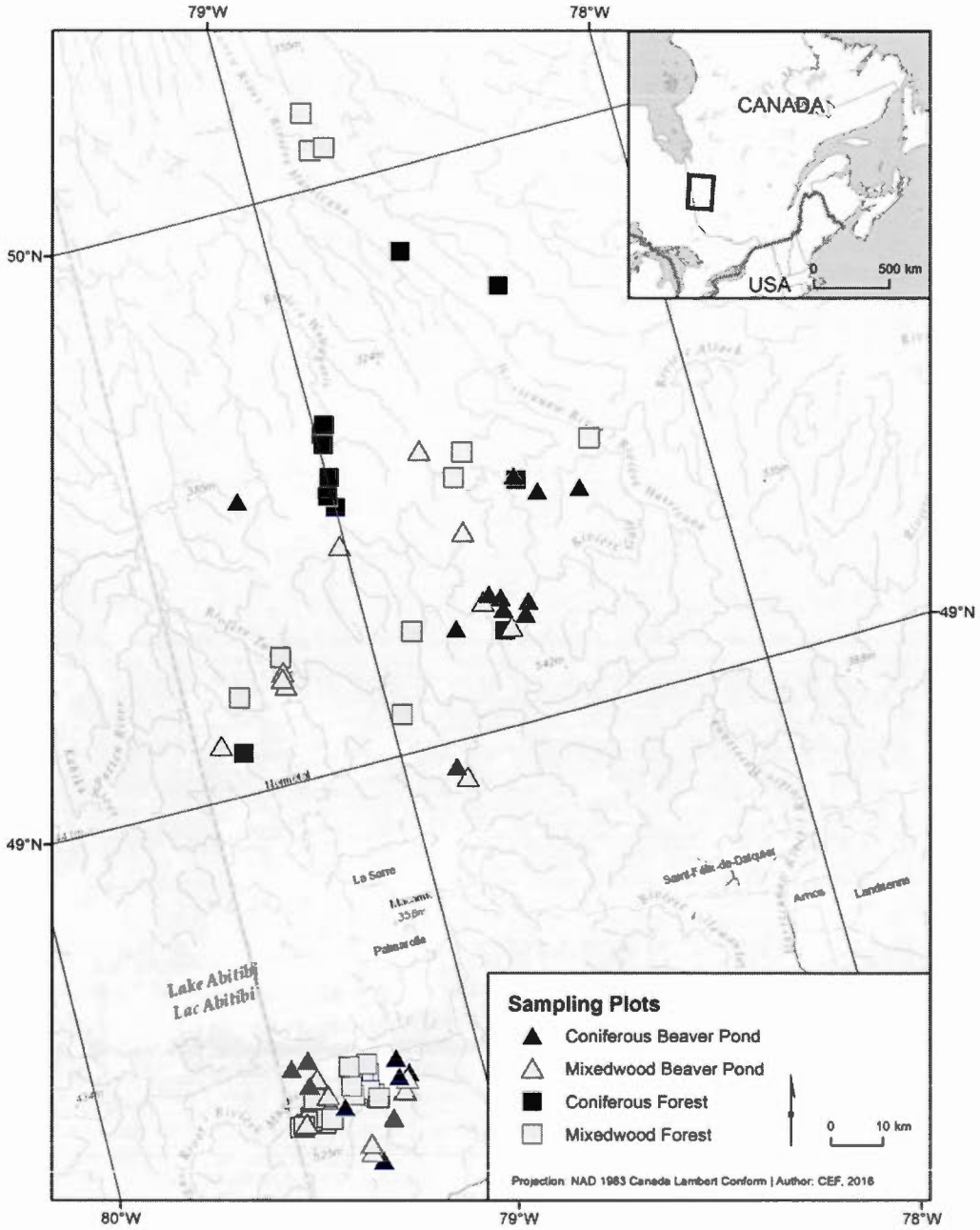


Figure 2.1. Location of sampling plots in northwestern Québec, Canada.

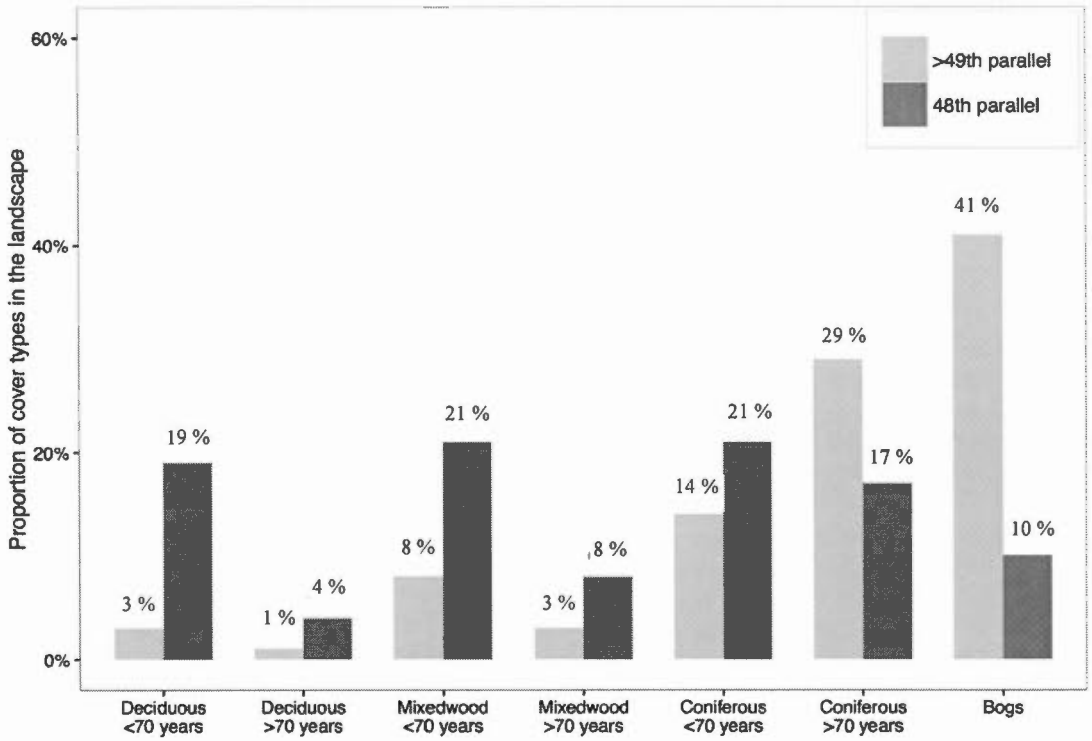
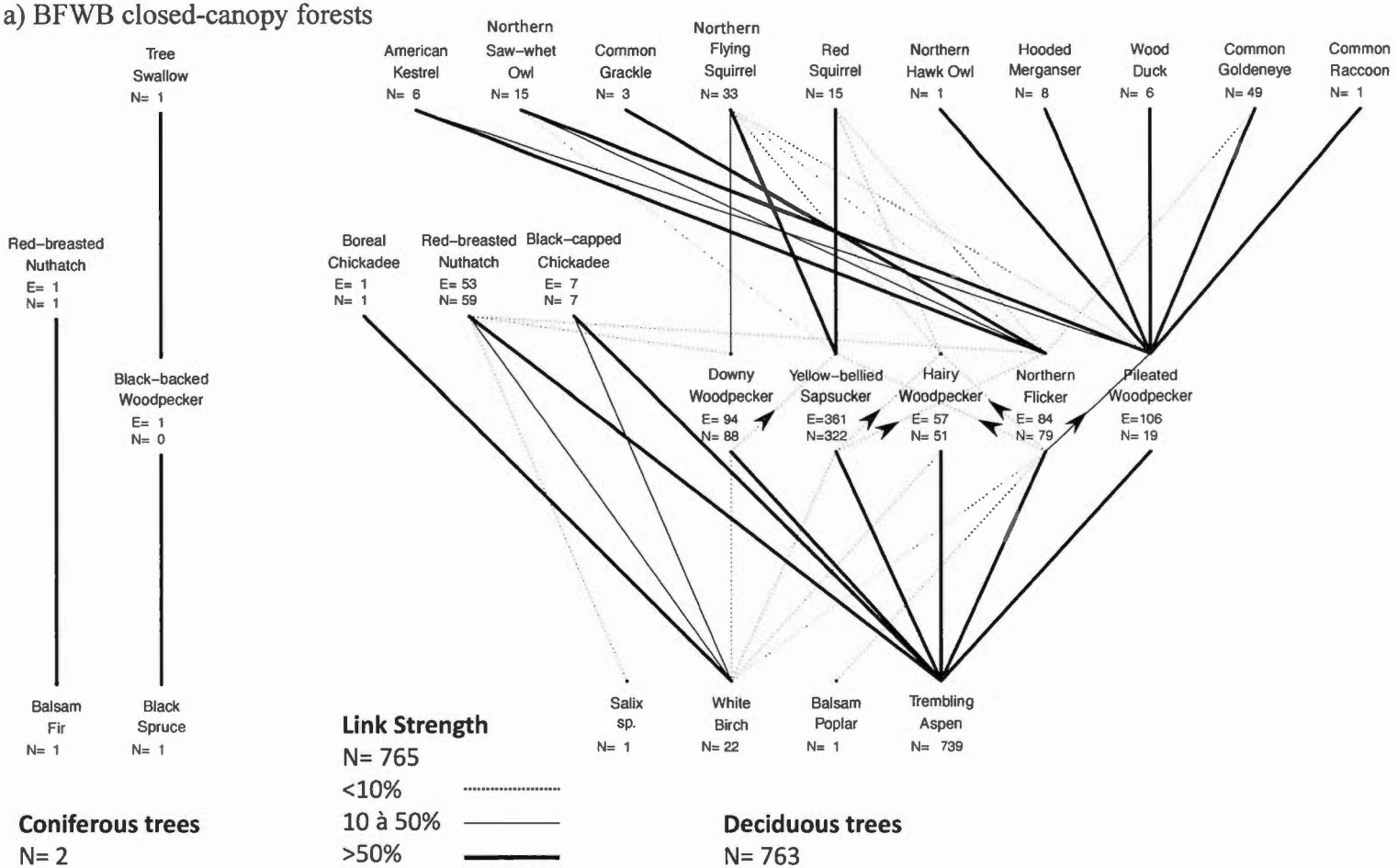


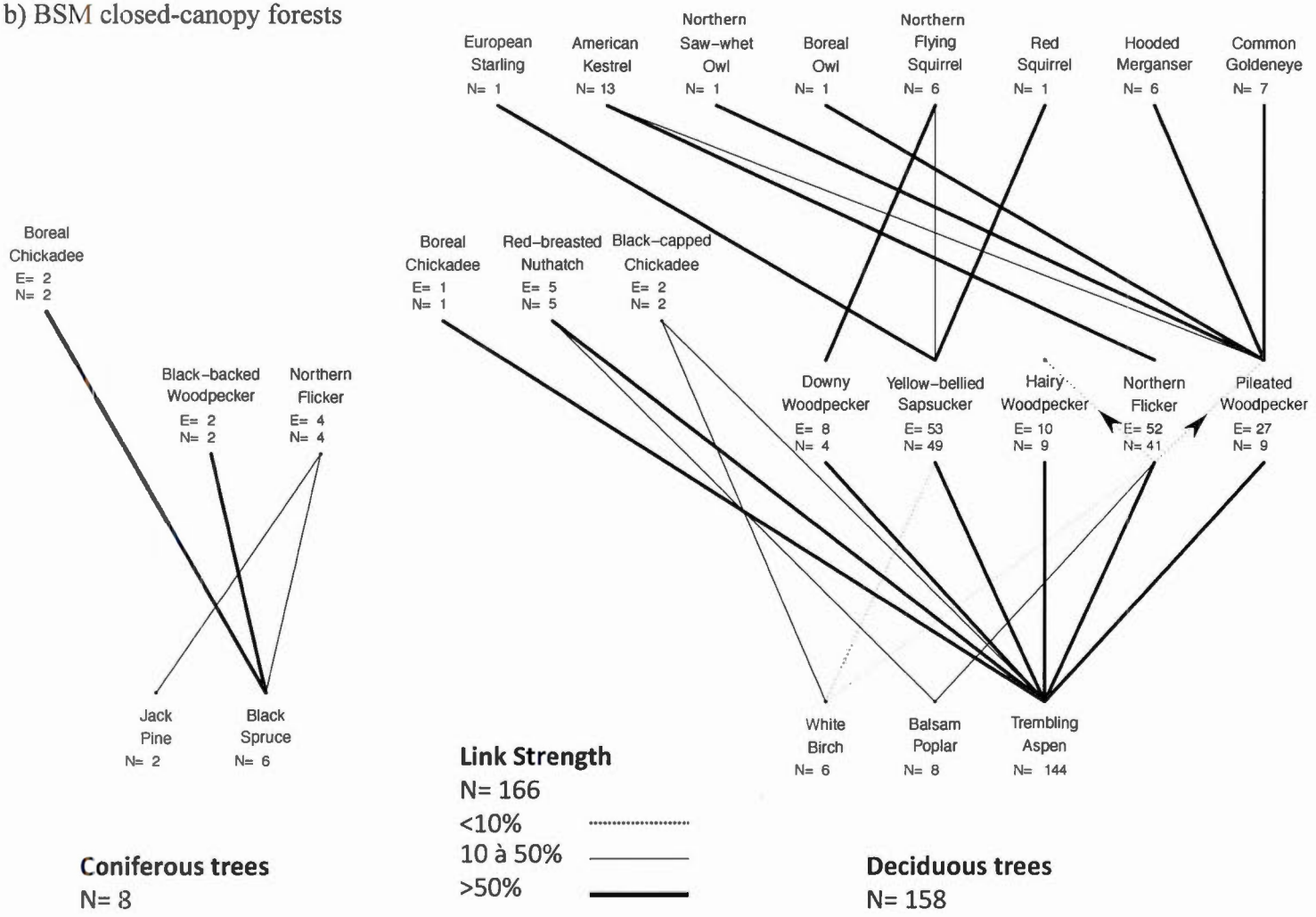
Figure 2.2. Proportion of cover types for BSM (north of the 49th parallel) and BFWB (48th parallel) in northwestern Québec, Canada.

Figure 2.3. Nest webs for a) BFWB closed-canopy forests, b) BSM closed-canopy forests, c) BFWB beaver ponds, and d) BSM beaver ponds in northwestern Québec, Canada. Nest data were collected from 2003 to 2015 for BFWB and from 2012 to 2013 for BSM. Lines between species represent the use of cavity resource. N is the number of occupied cavities found and E is the number of excavated cavities that were used by the excavator and by other cavity nesters. Links between the excavator level and the tree level represent the proportion of occupied cavities found in the tree species and the links between secondary cavity nesters, and excavators represent the proportion of nests or presence of mammals found in reused cavities. Reuse of cavities by excavators is indicated by lines between the base of the excavator that reused the cavity and the top of the excavator that created the cavity.

a) BFWB closed-canopy forests



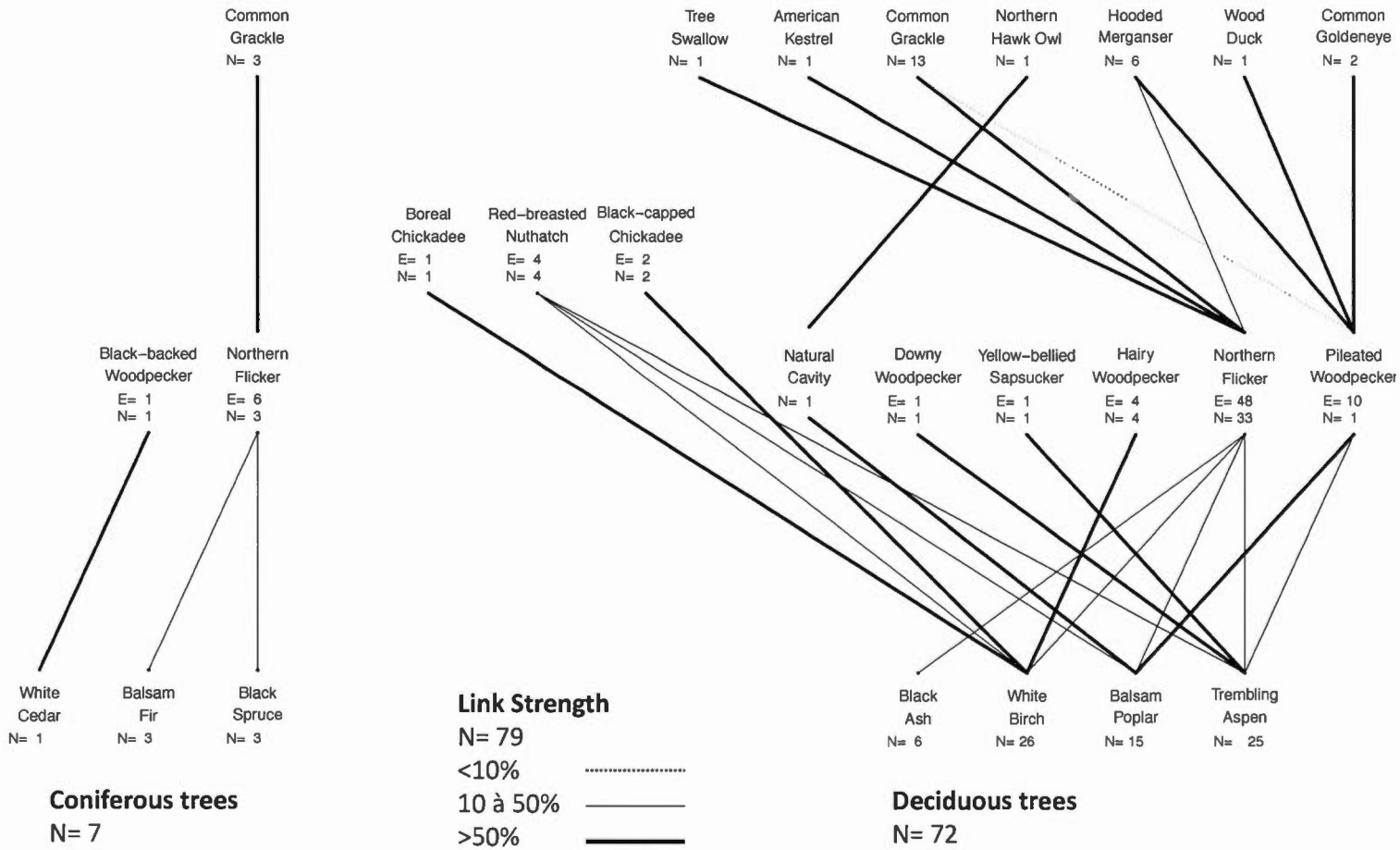
b) BSM closed-canopy forests



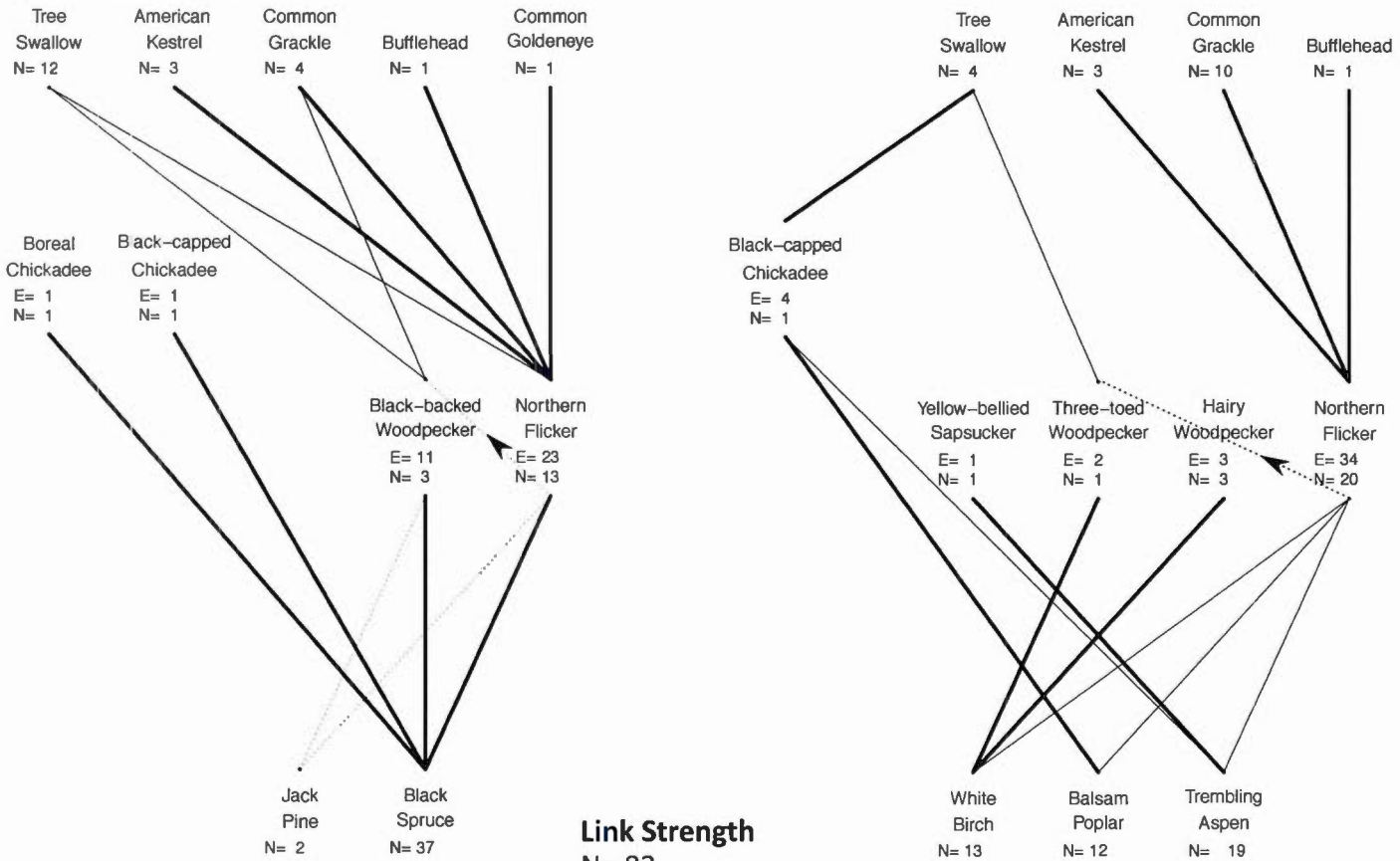
Coniferous trees
N= 8

Deciduous trees
N= 158

c) BFWB beaver ponds



d) BSM beaver ponds



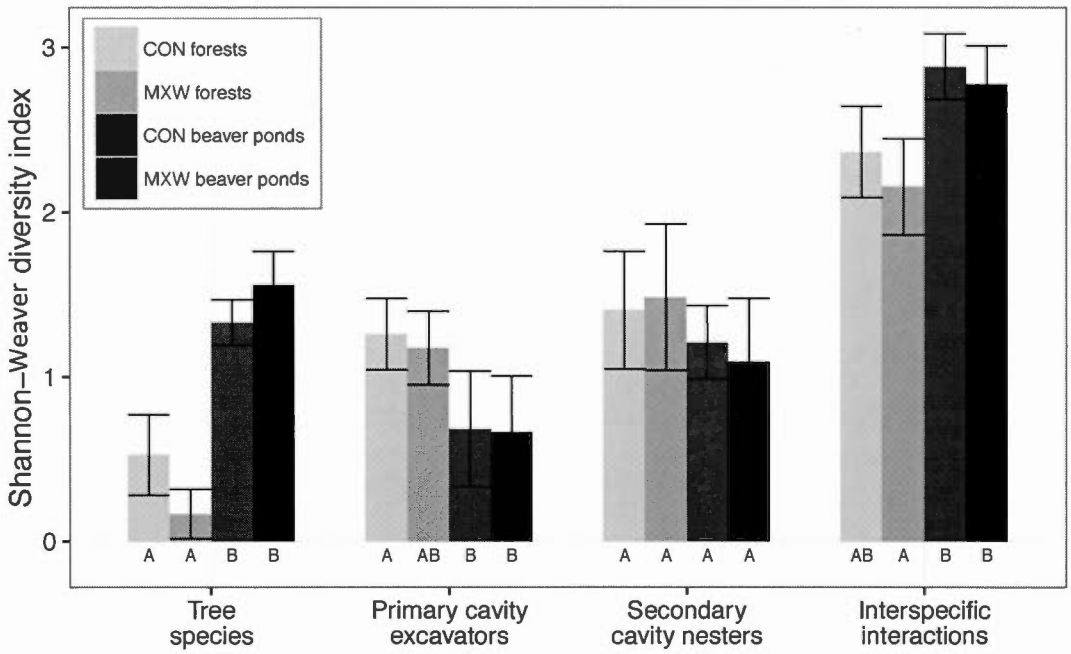


Figure 2.4. Means and 95 % confidence intervals of Shannon-Weaver diversity index for nest webs characteristics of BSM forests and beaver ponds and of BFWB forests and beaver ponds. We compared the diversity of cavity tree species, woodpecker species, secondary cavity nester species and interspecific interactions. The bootstrap procedure is described in section 2.4.6.3. Differences between habitats were considered significant when the 95 % confidence intervals did not overlap. These are indicated with letters.

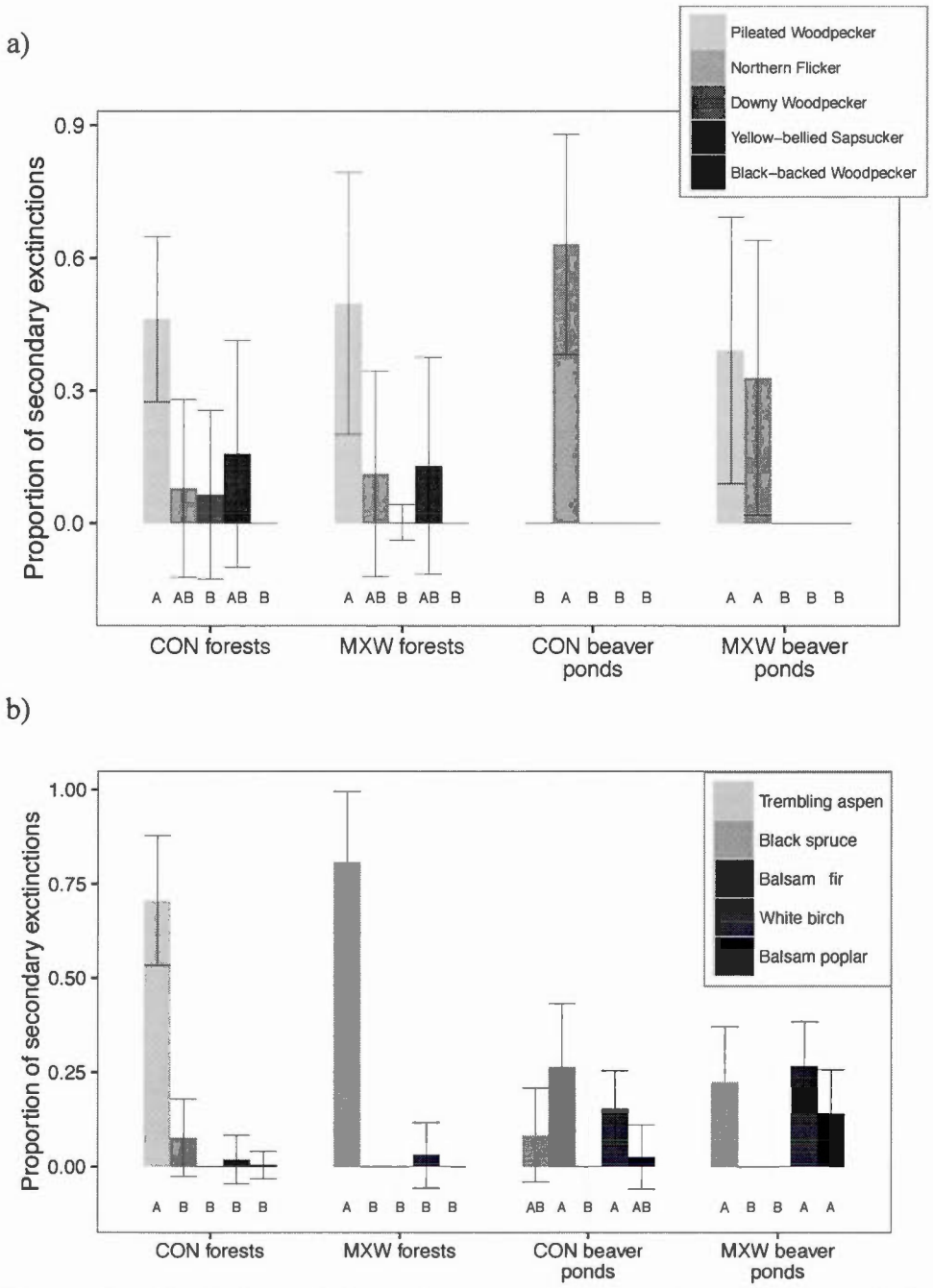


Figure 2.5. Evaluation of the robustness of nest webs to the loss of a) excavator species and b) tree species in BSM forests and beaver ponds and in BFWB forests and beaver ponds. We show the means and 95 % confidence intervals of the proportion of species loss due to the simulation of targeted species removal. Differences between habitats were considered significant when the 95 % confidence intervals did not overlap. These are indicated with letters.

2.11 Appendix A.

We contrasted the proportions of cavity trees having hard wood, heart rot and equally degraded wood in forest flooded by the American beaver and in closed canopy forests.

The majority of cavity trees in our subsample of trees examined for wood hardness showed important signs of wood decay (93 %) and had either heart rot at the DBH (54 %), equally degraded wood at the DBH (28 %) or the presence of fungal conks (59 %) (Table 2A). Most live cavity trees (89 %) and half of dead cavity trees (53 %) had fungal conks. In beaver ponds most cavity trees had either heart rot (48 %) or had equally degraded wood (48 %) whereas, the presence of fungal conks was only found on 26 % of cavity trees (Table 2A).

Table 2A. Proportions of cavity trees having hardwood, heart rot and equally degraded wood in forest flooded by the beaver and in closed canopy forests. Wood hardness was measured by coring the tree at breast height on a subsample of cavity trees found. Trees were classified as living or dead and inspected for fungal conks.

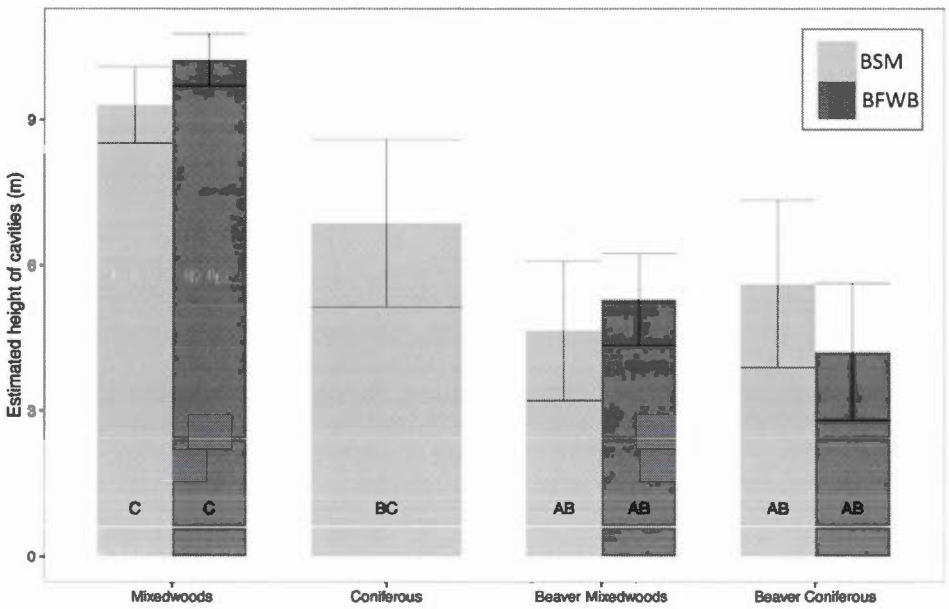
	Cavity trees in beaver ponds				Cavity trees in closed-canopy forests			
	Dead trees		Live trees		Dead trees		Live trees	
Wood hardness	w/o fungal conks n=20	with fungal conks n=7	w/o fungal conks n=0	with fungal conks n=0	w/o fungal conks n=32	with fungal conks n=37	w/o fungal conks n=5	with fungal conks n=39
Hard wood (%)	4	0	0	0	6	6	2	10
Heart rot (%)	33	15	0	0	11	17	3	25
Equally degraded wood (%)	37	11	0	0	11	10	0	0

2.12 Appendix B.

We compared cavity height between habitat types and regions with linear mixed models in which *Plot* was added as a random effect. For trees with multiple cavities we used the mean cavity height in order to only have one measure per tree. We used a theoretical-information approach using Akaike information criterion adjusted for small samples (AIC_c) to select the most parsimonious model between a model containing the habitat variable and a null model which included only the intercept. Model averaged predictions were performed using the AICcmodavg R package version 2.0 (Mazerolle 2015). We used the modavgEffect function of the R package AICcmodavg to verify if the confidence intervals included zero for every combination of habitats.

Cavity height strongly differed by habitat types (AIC_c = 2958.31, log-likelihood = -1469.98, w_i=1, null model's ΔAIC_c = 50.57; Figure 2B). Mixedwoods had the highest mean height with 10.2 m for BFWB region and 9.3 m in the BSM region followed by 6.9 m for coniferous forests (Figure 2B). Beaver ponds had the lowest mean cavity height ranging from 4.2 to 5.6 m (Figure 2B).

Figure 2B. Model averaged prediction of mean cavity height (m) for open and closed canopy forested habitat in the two regions (BSM = black spruce-moss region, BFWB = balsam fir-white birch region). Significant differences are indicated with letters.



CHAPITRE 3

THE PILEATED WOODPECKER (*DRYOCOPUS PILEATUS*): AN UMBRELLA SPECIES FOR CAVITY NESTERS IN BOREAL FORESTS

3.1 Résumé

Plusieurs chercheurs qualifient le Grand Pic (*Dyocopus pileatus*) d'espèce parapluie, c'est-à-dire que la conservation de son habitat serait aussi bénéfique pour plusieurs autres espèces. Par contre, il y a peu d'études empiriques sur le sujet. Nous avons évalué si la présence d'un arbre à cavité de Grand Pic peut être utilisée comme indicatrice de la qualité d'habitat de nidification de la faune cavicole en forêt boréale. Nous avons utilisé des données provenant d'une étude à long terme (2003-2014) couvrant un vaste territoire (12 000 km^2) qui recoupe les domaines bioclimatiques de la sapinière à bouleau blanc et de la pessière à mousses et où ont été récoltées dans 106 placettes d'échantillonnage des données sur la reproduction de la communauté cavicole. Contrairement aux autres études d'espèces indicatrices qui utilisent principalement des données d'occurrence, nous avons utilisé des données d'activité de reproduction (arbres de nidification) ce qui reflète plus directement les ressources limitant le plus ce groupe fonctionnel d'espèces. Nous comparons l'efficacité d'utiliser le Grand Pic par rapport à d'autres excavateurs pour prévoir la richesse en espèces cavicoles. Nos résultats montrent que le Grand Pic sélectionne fortement les peuplements qui sont sélectionnés par la grande majorité des utilisateurs de cavités : les vieux peuplements de forêts mixtes avec peupliers faux-trembles. Le Grand Pic est l'espèce dont la présence d'une cavité à un site est la plus susceptible de prévoir la présence de cavités de nidification des autres espèces cavicoles. De plus, son modèle de sélection d'habitats est celui qui explique le mieux la richesse des autres espèces cavicoles et il s'avère être le plus efficace pour prioriser les sites pour la conservation de ce groupe d'espèces. Le Grand Pic peut donc être considéré comme une espèce parapluie pour ce qui est de la qualité de l'habitat de reproduction de l'ensemble de la communauté cavicole, un compartiment clé de la biodiversité en forêt boréale.

3.2 Abstract

Several researchers and wildlife managers qualify the Pileated Woodpecker (*Dryocopus pileatus*) as an umbrella species or indicator species. The conservation of its habitat would also benefit multiple other co-occuring species. However, there are few empirical studies on the subject. We evaluated if the presence of a Pileated Woodpecker cavity tree can be used as an indicator of habitat quality for the reproduction of cavity nesters in boreal forests. We used data from a long-term study (2003-2014) which covers a vast territory (12 000 km^2) and overlaps two bioclimatic domains: the balsam fir white birch and the black spruce moss in eastern Canada. Data on the reproduction of cavity nesters were collected in 106 plots. Contrary to other indicator species studies that generally use occurrence data, we used nesting trees, which more directly reflects the limiting resource for this functional group of species. We compared the efficiency of using the Pileated Woodpecker over other cavity excavators for predicting cavity nesters species richness. Our results show that the Pileated Woodpecker strongly selects stands that are also selected by the majority of cavity nesters: old mixedwoods with trembling aspen. The Pileated Woodpecker is also the species for which the presence of its cavities at a site was the most susceptible to predict the presence of other species' nesting cavities. Moreover, its habitat selection model best predicted cavity nester species richness and was the most efficient for prioritizing sites for the conservation of this group of species. The Pileated Woodpecker can thus be considered an efficient umbrella species for the quality of breeding habitat for cavity nesters associated with mixedwoods, a key component of biodiversity in boreal forest ecosystems.

3.3 Introduction

Old forests and the keystone structures they contain, large old trees, are lost at an alarming rate everywhere in the world (Noss 1999, Lindenmayer et al. 2012, Lindenmayer et al. 2014). In the boreal forest, the proportion of old forests, which was historically regulated by natural disturbances, is now, in large part, also under the influence of forest management (Cyr et al. 2009, Drapeau et al. 2009a). This widespread influence of the human footprint throughout the boreal ecosystem has drastically changed the age structure of the forest cover, increasing the proportion of early-seral habitats while significantly decreasing the amount of old forests with regards to their historical importance (Esseen et al. 1997, Angelstam 1998, Bergeron et al. 2002, Bergeron et al. 2007, Cyr et al. 2009, Drapeau et al. 2009a). Accordingly, several studies have shown that organisms associated with old forests are affected by the large-scale loss of this habitat type in managed landscapes (Niemi et al. 1998, Drapeau et al. 2000, Kouki and Väänänen 2000, Schmiegelow and Mönkkönen 2002, Venier et al. 2014). Fulfilling the long-term maintenance of biodiversity in the boreal forest thus greatly relies on conservation planning of old forest habitats in the managed matrix (Drapeau et al. 2009a, Villard and Jonsson 2009).

Approaches to ensure the retention of old forest habitats within boreal managed landscapes to maintain biodiversity are thus of paramount importance as the size of the human footprint in the boreal forest increases (Hansen et al. 2013, Gauthier et al. 2015). While the conservation of all native species in managed landscapes raises challenges about the appropriateness of using traditional single-species approaches, the urgency to act in a context of limited funding and knowledge on complex ecological systems has fostered the development of concepts such as the umbrella species concept (Lambeck 1997, Fleishman et al. 2001, Roberge and Angelstam 2004). In short, this concept proposes that the conservation of the habitat for the umbrella species would also benefit multiple other species. This approach has the

potential of concentrating and simplifying conservation efforts but runs the risk of oversimplifying complex ecological problems. It is argued that a single species cannot take into account all other species habitat requirements. To remedy this, Lambeck (1997) proposed using a suite of focal species, in which each species would reflect certain habitat requirements. Lambeck's focal species approach uses species that are the most vulnerable to a threat to quantify the habitat conservation.

In the boreal forest, the cavity-nesting and roosting community represents a high proportion of vertebrates that relies on old forest habitats and its key structural elements: decaying and dead trees (Martin and Eadie 1999, Cadieux 2011, Cooke and Hannon 2012, Nappi et al. 2015). Many of these species have been identified as sensitive to forest management (Imbeau et al. 2001). Among those, woodpeckers are a keystone group as they are engineers at the base of the creation of most cavities that provide critical roosting and breeding conditions to most secondary cavity users in the boreal forest (Bednarz et al. 2004, Cockle et al. 2011). However, to do so they require adequate trees for excavation, which have a large diameter and are senescent or dead. In addition, the majority of woodpecker species in the boreal forest also rely on senescent or dead trees for foraging (Nappi et al. 2015). Their habitat requirements and sensitivity to forest management makes them good candidates for being indicator species of forest health and bird diversity (Mikusiński et al. 2001, Roberge and Angelstam 2006, Virkkala 2006, Drever et al. 2008, Drever and Martin 2010). In western Canadian mixedwoods, Drever et al. (2010) verified whether woodpecker species are associated with the same habitat variables in order to assess if woodpeckers can be managed as a suite of species using the same habitat targets. They conclude that besides the Black-backed Woodpecker (*Picoides arcticus*) and the American Three-toed Woodpecker (*Picoides dorsalis*), these species can be managed as a single suite of species since no strong trade-offs appear to exist between them. However, conservation aimed at the general level of woodpecker species richness might leave some of the most demanding cavity nester species behind.

In this study, we assess if the Pileated woodpecker (*Dryocopus pileatus*) can be a good indicator of breeding habitat quality of cavity users in boreal forests since it is the most demanding species in terms of the nest tree. Being the largest woodpecker species in North American forests, the Pileated woodpecker requires large senescent or dead trees for nesting, roosting and foraging, which are only common in old forests (McClelland et al. 1979, Bull et al. 1992, McClelland and McClelland 1999, Savignac et al. 2000, Aubry and Raley 2003, Lemaître and Villard 2005, Cadieux 2011, Cooke and Hannon 2012, Nappi et al. 2015). Furthermore, its role as a keystone species in nest webs for large secondary users is well established (Bonar 2000, Aubry and Raley 2002, Martin et al. 2004, Cadieux 2011, Cooke and Hannon 2011). Its large home range also puts it in line with the initial definition of umbrella species, where species with large home ranges were favored as umbrella species since the conservation of their area requirement would also convey protection for multiple species with smaller home ranges (Wilcox 1984, Roberge and Angelstam 2004).

Several researchers and wildlife managers qualify the Pileated Woodpecker as an umbrella or indicator species and use this species as part of a suite of focal or umbrella species (Bull et al. 1992, Blanchette and terrestre 1996, McLaren et al. 1998, Savignac et al. 2000, Aubry and Raley 2003, Lemaître and Villard 2005, Cheveau 2015). McClelland et al. (1979) proposed that conservation efforts aimed at the habitat of the Pileated Woodpecker would also conserve habitats for most cavity nesters, as this excavator was strongly associated with old-growth forests in forests of northwestern Montana, United States. Even though this species is widely used to this effect, to our knowledge no study has evaluated empirically the assumption that the Pileated Woodpecker is an umbrella species for the cavity-nesting community. In fact, as highlighted by Roberge and Angelstam (2004), only a few studies have demonstrated empirically the efficiency of the umbrella species concept (see Branton et Richardson 2011 for a recent review). Moreover, these studies have mainly used

species occurrence data to make inferences on the potential habitat use by other species. Co-occurrence patterns of species do not allow, however, assessing habitat quality of both the umbrella and its underlying group of species. To do so one needs to focus on habitat attributes that provide a proxy for assessing the fitness of individuals of both the indicator and the response group of species. For the cavity-nesting community, using data of active nest trees focuses on the most demanding and limiting resource (Newton 1994), which is a more direct information for evaluating how habitat quality for the cavity-nesting community is tied with habitat quality of the Pileated Woodpecker.

To evaluate the potential of the Pileated Woodpecker to be an umbrella species for the cavity-nesting and roosting community we first compare the Pileated Woodpecker's selection of nesting habitat with nesting habitat selection by other woodpeckers and cavity-nesting species to assess how this species fulfills the assumption of being strongly associated with highly coveted habitat resources by other species (Roberge and Angelstam 2004, Roberge et al. 2008). Second, we measured the cavity nester species richness associated with the presence of Pileated Woodpecker's cavity trees in forest stands. Our assumption is that an umbrella species should show high co-occurrence with other species (Fleishman et al. 2000). Finally, using a simulation approach, we evaluate the efficiency of the Pileated Woodpecker habitat selection model to predict cavity nester species richness (Fleishman et al. 2001, Roberge and Angelstam 2004).

3.4 Methods

3.4.1 Study area

Our study was conducted along a latitudinal gradient of 200 km in the boreal forest of northern Quebec (Figure 3.1). It was located in the northern Clay Belt of Quebec and Ontario and overlapped two bioclimatic domains: the balsam fir-white birch

mixedwood region (BFWB) and the black spruce-moss, a conifer dominated forest region (BSM) (Robitaille and Saucier 1998). The BFWB region is characterized by clay soils and low rocky hills (Robitaille and Saucier 1998). The area contains a complex natural forest mosaic formed by different forest cover types and by a variety of natural disturbances (Harvey 1999). The BSM region has a generally flat topography and therefore has a greater tendency for paludification (Robitaille and Saucier 1998). The forest mosaic is dominated by black spruce stands (Gauthier et al. 2000).

The data was collected from 2008 to 2015 in 106 plots ranging from 0.5 to 30 ha (total area = 783 ha) in forests considered quality habitat for cavity users. Closed-canopy forests were a mixture of mature and old forest stands enclosed in a continuous forest matrix and in a managed landscape (n = 86). Open-canopy forests were forests flooded by the action of the beaver (n = 20). The numerous plots and type of habitat sampled represented well what was found at a landscape scale and were well suited to help us evaluate the Pileated Woodpecker as an umbrella species for cavity nesters as a whole.

3.4.2 Cavity search and nest monitoring

Cavity tree data was collected using cavity and nest search surveys and cavity monitoring using the same protocols throughout the years. Every plot was surveyed for two years. During the first year, we searched for cavities and nests and during the second year, those cavities were inspected to assess breeding or roosting activity. In forests plots, we positioned line transects every 50 m that were visited twice. Nest searches were conducted between the beginning of May and the middle of July. Observers walked along line transect and used visual and auditory cues to detect the presence of an occupied cavity: breeding-bird behavior, begging nestlings or wood chips on the ground. In beaver ponds, a different survey protocol was elaborated. Instead of following transects, every tree in the pond was inspected for cavities with a

canoe and high boots. All trees with cavities were marked with an aluminum tag and geo-referenced. These cavities were inspected with a camera mounted on a telescopic pole (TreeTop Peeper™, Sandpiper Technologies, Manteca, California) to determine the state of the cavity (unfinished cavity or fully excavated nesting cavity). A cavity was considered "occupied" if it contained at least one egg or one nestling, or if a mammal was present inside the cavity. The excavator of the cavity was visually identified. However, Pileated Woodpecker cavities were also identified with the characteristics of the cavity since these large cavities are easily distinguished from other excavating species. These cavities are typically egg-shaped and are almost twice as large as the Northern Flicker's, the second-largest cavity excavator found in the study area after the Pileated Woodpecker (Bertrand, Cadieux and Drapeau unpublished data, Martin et al. 2004).

3.4.3 GIS data preparation and sampling

Digital forest cover maps were used for delimiting forest stand boundaries and vegetation stand characteristics (Ministère des Ressources naturelles et de la Faune, 2011). This ensured that our results would be easily applicable by forest managers. We used the geographic information system softwares QGIS (Quantum GIS Development Team, 2014) and GRASS (GRASS Development Team, 2015) in combination with R (R Development Core Team, 2015). These maps were updated to include recent changes in land cover since the creation of the maps. The sampling plots were superimposed on the digital forest cover maps. The polygons of the digital forest cover maps were clipped so that only those inside the plots remained. We attached the cavity tree data to the polygons. The clipping of the digital forest cover maps by the sampling plots resulted in many small polygons. To eliminate these and reduce the number of polygons we only used polygons larger than 0.05 hectares, which kept 99.5 % of nests found (2 polygons with nests and 281 without nests were discarded resulting in a total of 577 polygons). Locations of cavity trees were verified in the field and with digital forest cover maps.

3.4.4 Statistical analyses

We verified the effectiveness of using the presence of a Pileated Woodpecker cavity tree and the Pileated Woodpecker habitat selection to identify species rich closed-canopy forest stands. We compared the Pileated Woodpecker's performance to other excavators and to null models. The statistical unit was the forest polygon and species richness referred to the number of species with an active cavity in the polygon. Analyses were performed with R version 3.2.3 (2015) and graphics were created with the R package: ggplot2 (Wickham et al. 2013).

3.4.4.1 Habitat specificity and selection by cavity nesters

Using nesting and roosting cavity trees data collected at a regional scale, we first measured the association of cavity user species to open and closed-forest habitats. This allowed us to build a list of expected beneficiary species, species that have the potential of benefiting from the conservation of closed-forest habitats (Roberge and Angelstam 2004, Roberge et al. 2008) and to measure the degree to which Pileated Woodpecker and other excavators are specialized to closed-canopy forests, since umbrella species should not be generalists (Fleishman et al. 2000). Polygons were classified in two habitat categories using the height of the forest stands: > 10 m for mature and old closed canopy forests (MOCC) and < 10 m for young and open canopy forests. The habitat specificity was calculated with presence only data (at least one cavity or nest tree) as the proportion of polygons classified in either habitat category. All species having at least one cavity or nest tree located in MOCC were used to build a list of expected beneficiary species.

To assess how the Pileated Woodpecker fulfills the assumption of being strongly associated with highly coveted habitat resources by other cavity nester species we determined habitat selection parameters for the Pileated woodpecker and verified if they were similar for most cavity nesters. To achieve precise habitat suitability models (HSMs) and to steer this study towards conservation of critical habitat, we

limited this analysis to MOCC which consisted of 307 polygons covering 593 ha. Habitat selection models were tested for the following excavators: the Pileated Woodpecker, the Yellow-bellied Sapsucker (*Sphyrapicus varius*), the Downy Woodpecker (*Picoides pubescens*) and the Northern Flicker (*Colaptes auratus*), in which the response variable was the presence or absence of a cavity tree in the polygon. Ten expected beneficiary species did not have enough occupied polygons for the analysis ($\leq$ 20 polygons). These species were grouped as "grouped cavity users" and their habitat preferences were modeled with the same candidate models. However, the species richness was used as the response variable.

We tested a series of HSMs at the stand and landscape scale. The models were comprised of habitat variables derived from digital forest cover maps and that were considered important for cavity nesters (Table 3.1). Some variables were highly correlated ($r > 0.7$) and were not included in the same models (Aspen - Height and Aspen - Conif). To limit the number of models, we used a hierarchical modeling approach (Table 3.2). First, models with habitat variables at the stand level were compared. The best models were selected when a $\Delta AIC_c < 2$ (Burnham and Anderson 2002). These were then combined with variables at the landscape scale one at a time (Table 3.2). A radius of 700 m (154 ha) was used as the surrounding area size for the landscape scale. This area size was chosen because it incorporates most cavity nesters home ranges. To measure the variables at the landscape scale, digital cover maps were rasterized at a scale of 20 x 20 m in a binary format for the landscape variables of interest (Table 3.1). Then, we performed a focal cell analysis using the r.neighbors function in GRASS which attached the average value of all cells contained in a 700 m radius to the focal cell. Finally, we used the function v.rast.stats in GRASS to calculate the mean value of the landscape variable for each polygon. The diversity of tree species in the landscape was calculated using the Shannon-Weaver diversity index on the frequencies of dominant or co-dominant tree species.

We used generalized mixed models (GLMMs) with Plot as a random effect and polygon Area as offset in each model (Bates et al. 2015). GLMMs with binomial error distribution and a complementary log-log link were used for single species models. GLMMs with a Poisson error distribution and log-link function were used to identify habitat resources influencing the grouped cavity users. Over-dispersion was tested for the latter models. We used a theoretical-information approach using Akaike information criterion adjusted for small samples (AIC_c) to compare candidate models and to select the most parsimonious (Mazerolle 2015). Models having a $\Delta AIC_c < 2.0$ were considered as having strong support. In addition, a pseudo-R^2 based on the likelihood-ratio test was computed for each model with the r.squaredLR function from the R package MuMIn (Barton 2015). This allowed us to specify the null model that contained the random effects and the offset. We did bootstraps with a rotation of 1000 samples to predict the probability of presence of cavity trees for every polygon and to estimate parameters and 95 % confidence intervals (Bates et al. 2015). For individual species, we evaluated the fit of the bootstrapped predictions using Cohen's Kappa statistic. To evaluate the fit of the predictions for the species richness, we use a linear regression and Spearman's correlation index on the observed data versus the predicted data (Potts and Elith 2006). Best models were verified for uninformative parameters and models containing such parameters were dismissed (Arnold 2010). Best models with uninformative parameters are generally copies of higher ranked models with the addition of non-significant variables (Arnold 2010). We identified uninformative parameters with 85 % confidence intervals computed through bootstraps with 1000 permutations as proposed by Arnold (2010). Furthermore, if models were closely competing, we chose the model with the highest Kappa value.

3.4.1.2 Co-occurrence analysis

We calculated and compared mean cavity user species richness for polygons occupied by the cavity trees of the Downy Woodpecker, the Yellow-bellied Sapsucker and the Pileated Woodpecker. We limited this comparison to excavators with the potential of

being umbrella species: these had to be specific to MOCC and had to have enough occupied polygons to calculate precise means (≥ 20 polygons). In addition, the mean species richness was calculated for all polygons to represent a null model. Nests of the excavator in question were not included in the species richness estimate. To take into account the hierarchical structure of the sampling design, we used generalized mixed models (GLMMs) with Plot as a random effect and polygon size was added to the model as an explanatory variable (Bates et al. 2015). Means and 95% confidence intervals were estimated for one excavator at a time and compiled. We used the function bootMer from the R package: Lme4 to perform bootstraps with a rotation of 1000 samples to predict the species richness and 95 % confidence intervals (Bates et al. 2015). Means were predicted for a polygon size of 3 hectares, which was the average size of polygons with at least one occupied cavity. We calculated means for three levels of species richness: a) all expected beneficiary species, b) cavity excavators and c) secondary cavity nesters.

3.4.1.3 Simulations of site selection with potential umbrella species

These analyses simulate the selection of sites for conservation of cavity nesters with the concept of the umbrella species. We assess the efficiency of using HSMs of cavity excavating species to select sites with high cavity nesters' species richness. We focus on excavators that were specific to MOCC and that could be adequately modeled with habitat variables. Three excavators were selected for having a good fit between the observed and predicted values calculated with the HSMs: the Downy Woodpecker, Yellow-bellied Sapsucker and the Pileated Woodpecker (kappa values > 0.35).

First, we compared species accumulation curves to assess the efficiency of prioritizing sites for conservation of cavity nesters with excavator HSMs. This analysis was chosen because of its sensitivity to rare species. Sites selected with an umbrella species should accumulate species more efficiently, or with less accumulated sampled area, than a site selection made with other species or a random

site selection since the umbrella species habitat requirements are thought to include the habitat requirements of the beneficiary species (Fleishman et al. 2001). We present species accumulation curves called « collectors curve » in which the observed species accumulation is conditional to a specified order of samples. For selected excavators, all polygons were ordered by the probabilities of presence of cavity trees predicted with the HSMs. We compare these curves to a randomly sampled curve with 95 % confidence intervals. We used the r package vegan with the *Specaccum* function and took into account the sampling effort (the size of polygons) (Oksanen et al. 2013). The accumulation curves were plotted against the polygon area size accumulation. When the collector's curve is not included in the random curve it is considered significantly different from a random selection of polygons. We built curves for three levels of species richness: a) all expected beneficiary species, b) cavity excavators and c) secondary cavity nesters (see Table 3.3 for a list of expected beneficiary species).

Second, we compared the potential of each of our selected excavator species in predicting cavity nester species richness. In this case, the nests of the focal excavator were removed from the response variable (species richness). Once again, three levels of species richness were compared. Each excavator was assigned its predicted probability of presence based on its HSM. GLMMs with a Poisson error distribution and log-link function were used to identify which excavators better predicted cavity nester species richness (Bates et al. 2015). The variable Plot was added as a random effect. Since the index was positively skewed (many sites having low predictions), we compared the index data to a log transformed index to maximize the linearity between dependent and independent variables. Over-dispersion was tested for all models. A pseudo-R^2, as described in the earlier section, was computed for each model in which the null model contained the offset of polygon size (Barton 2015). We used bootstraps with a rotation of 1000 samples to predict mean species richness and 95 % confidence

intervals and to estimate fixed and random coefficients with 95 % confidence intervals (Bates et al. 2015).

3.5 Results

Between 2008 and 2015, we found 425 nests or occupied cavities for 18 cavity-nesting species. The majority of cavity trees were in trembling aspen (84 %). Out of 577 polygons (778.8 ha), 191 had at least one cavity tree and 149 contained at least one nest or occupied cavity (Table 3.3).

3.5.2 Habitat specificity and selection by cavity nesters

A majority (79 %) of polygons with the presence of cavity trees were in MOCC. Fourteen species were found in forests with a height > 10 m and thus, made up the list of expected beneficiary species for an umbrella species specialized on closed canopy mature and old boreal forests (Table 3.3). Four species were only found in open forested habitats or in young forests (< 10 m) (Table 3.3). Most excavators were present in MOCC polygons. Of these, the Downy Woodpecker, the Yellow-bellied Sapsucker, the Hairy Woodpecker (*Picoides villosus*) and the Pileated Woodpecker were the most specific to MOCC habitat (Table 3.3). The Northern Flicker had poor habitat specificity with 55 % of stands in MOCC (Table 3.3). Few nest trees were found for the Black-backed Woodpecker (*Picoides arcticus*) and the American Three-toed Woodpecker (*Picoides dorsalis*). However, nests found opportunistically were mostly located in open forested habitat (< 10 m) (see chapter 2).

The Pileated woodpecker strongly selected habitat resources also selected by other cavity nesters (Table 3.4, Table 3.5). Woodpeckers and other cavity-nesting species selected stands with trembling aspen whereas all best models contained a positive relation with the proportion of trembling aspen (Table 3.4, Table 3.5). For the Pileated Woodpecker, the Yellow-bellied Sapsucker, the Northern Flicker and the grouped

cavity users, the best models also contained the interaction between the proportion of trembling aspen and the stand age, which indicated a preference for stands with trembling aspen that increased as the age of stand increased (Table 3.4). Also, for the Northern Flicker and the grouped cavity users, the model containing only the proportion of aspen was more parsimonious (Table 3.4).

Variables at the landscape scale (radius of 700 m) added strength to the models and allowed us to distinguish important differences in habitat selection between species (Table 3.4). The Pileated Woodpecker strongly selected old trembling aspen stands surrounded by a high diversity of tree species which was represented by the model with the interaction between the proportion of trembling aspen and the stand age, and the diversity of tree species in the landscape (Table 3.4, Table 3.5). This model was also among the best for the Yellow-bellied Sapsucker but was closely competing with the model that included the proportion of coniferous stands in the landscape with a negative relation (Table 3.4, Table 3.5). The presence of a Downy Woodpecker cavity tree was associated with a high proportion of aspen at the stand level and a high proportion of mixedwood stands in the landscape (Table 3.4, Table 3.5). Not surprisingly, the Northern Flicker, which was not specific to MOCC, was positively associated with stands with trembling aspen but also with young forests and forest cuts in the landscape (Table 3.4, Table 3.5). There were three closely competing models for the grouped cavity users. All of these models included the proportion of trembling aspen and two included the interactions between this tree species and the stand age (Table 3.4). These models contained a positive relation with the diversity of tree species in the landscape and a negative relation to the proportion of old forests in the landscape (Table 3.5). This negative relation with old forests in the landscape can be explained by the high proportion of old black spruce forests (> 120 years) in some areas of the study. These forests generally had very low productivity and were often affected by paludification.

Diagnostics of the bootstrapped predictions revealed an overall good fit between the observed and predicted data. Nevertheless, model fit between excavators was highest for the Pileated Woodpecker and the Yellow-bellied Sapsucker and lowest for the Downy Woodpecker and the Northern Flicker (Table 3.4). The prediction data for the grouped cavity users seemed to adequately predict the observed data (Table 3.4) and there was no evidence of overdispersion.

3.5.1 Co-occurrence analysis

While only 23 % of polygons had at least one nest, polygons with cavity trees had much higher proportions (Yellow-bellied Sapsucker - 63 %, Downy Woodpecker - 85 % and Pileated Woodpecker - 86 %). In addition, all expected beneficiary species were found in polygons with Pileated Woodpecker cavity trees and in polygons with Yellow-bellied Sapsucker cavity trees, while polygons with Downy Woodpecker cavity trees had 86 % of these species (see Table 3.3 for a list of expected beneficiary species).

The presence of Yellow-bellied Sapsucker, Downy Woodpecker and Pileated Woodpecker cavity trees in a polygon was associated with a higher cavity nester species richness than the null model, although for the Yellow-bellied Sapsucker, this relation only differed significantly for the secondary cavity nester species richness level (Figures 3.2a, b, c). The polygons with Pileated Woodpecker cavity trees had the highest mean cavity user species richness. It differed significantly from the null model and the Yellow-bellied Sapsucker but not from the Downy Woodpecker. As for the presence of Downy Woodpecker cavity trees, they were associated with higher species richness and differed significantly from the null model but not from the Yellow-bellied Sapsucker or the Pileated Woodpecker. This trend was similar to the secondary cavity user species richness and the cavity excavator species richness levels (Figures 3.2a, b, c). For the secondary cavity nester species richness level, the presence of a cavity tree from any of the three focal excavators had significantly

higher species richness than the null model. The estimated parameter values of the size of polygons on species richness are presented in Appendix 3.1.

3.5.3 Simulation of site selection with potential umbrella species

With a simulation of site selection for conservation of cavity users, we evaluated the efficiency of using three potential umbrella species: the Downy Woodpecker, the Yellow-bellied Sapsucker and the Pileated Woodpecker.

The Pileated Woodpecker HSM is the scenario where the conservation of sites was the quickest to reach the maximum number of species. Only 30 ha of the best-ranked stands for the nesting habitat of the Pileated Woodpecker were necessary to accumulate all of the expected beneficiary species (Figure 3.3a). In comparison, it took 130 ha for the Yellow-bellied Sapsucker and 180 ha for the Downy Woodpecker to achieve similar results. The random site selection species accumulation curve 95 % confidence intervals started to include all species at 114 ha (Figure 3.3a). These results were consistent for cavity excavators' species richness and secondary cavity nesters' species richness levels (Figures 3a, b, c).

Habitat selection models for the Downy Woodpecker, the Yellow-bellied Sapsucker and the Pileated Woodpecker were better than null models for predicting species richness as pseudo-R^2 ranged from 0.15 to 0.33 (Table 3.6). Nevertheless, the Pileated Woodpecker had the highest predicted species richness for all three species richness levels (Figure 3.4 and Table 3.6). Species richness was about twice as much in sites with high probabilities of finding Pileated Woodpecker's nest trees than in sites with high probability of finding Yellow-bellied Sapsucker's nest trees (Figure 3.4). Excavators HSMs had higher explanatory power when transformed to the logarithmic scale, suggesting an exponential relationship with species richness.

3.6 Discussion

The Pileated woodpecker can be considered an effective umbrella species in the boreal forest as it met several key criteria (sensu Roberge et al. 2008). To our knowledge, this is the first study to provide empirical evidence to this effect. Using data on nesting cavity trees which directly reflects the most demanding and limiting resource for cavity nesters, we showed that this excavator was specific to closed-canopy forests, had strong selection for resources which were also selected by other species for their nesting habitat, and was a good predictor of species-rich forest stands. In addition to being a keystone species with its creation of large cavities, and an indicator species for habitats of special conservation concern such as old mixedwood forests, the Pileated Woodpecker's cavity trees in forest stands were good predictors of habitat quality for the reproduction of the cavity-nesting community in the boreal forests.

3.6.1 Strong selection of highly coveted resources

The Pileated woodpecker was specific to closed-canopy forests and had a strong selection of highly coveted resources by the majority of cavity nester species. This strong selection for stands older than 80 years with trembling aspen coincided with the general decline of this tree species after 80 years (Bergeron et al. 1998). The Pileated Woodpecker selected the transitional stage where many large trembling aspen are senescent and dying, creating a high volume of dead wood and the opening of the canopy, thus creating a complex forest structure (Bergeron et al. 1998). However, the choice of a forest stand for excavating cavities and nesting was also influenced by landscape attributes as suggested by Savignac et al. (2000). The Pileated Woodpecker selected a mixture of forest stands with large decaying or dead trembling aspens for nesting and a higher diversity of tree species, including conifers, in the landscape (154 ha). This selection might be related to its foraging needs. Unlike the Northern Flicker which forages for ants on the ground (Elchuk et al. 2003)

and the Yellow-bellied Sapsucker that has been shown to use regenerating forests < 10 m to forage (Bédard 2013), the Pileated Woodpecker foraging activities have been linked to large decaying and dead deciduous and coniferous trees in mixedwood forests (Lemaître and Villard 2005, Gasse 2007, Nappi et al. 2015). In our study region, its foraging marks were most commonly found on large dead trees and on live but senescent white birch and white cedar, which are more common in old mixedwoods (Cadieux, unpublished data).

3.6.2 The Pileated Woodpecker: an umbrella species

The umbrella species habitat requirements should include the habitat requirements of the beneficiary species leading to an efficient conservation effort in which the ratio of costs (area conserved) versus benefits (number of beneficiary species protected) would be the smallest possible (Fleishman et al. 2001, Roberge and Angelstam 2004). Using simulations of site selection with the concept of the umbrella species, we demonstrated that a strategy aimed at conserving the Pileated woodpecker's preferred habitat is likely to conserve sites for cavity nesters more efficiently than other woodpecker species. The nesting habitat requirement of the Pileated Woodpecker seemed to include the nesting habitat requirements of most cavity nesters as it took only a small amount of accumulated sampled areas of the sites best ranked for the presence of the Pileated Woodpecker to reach the maximum number of cavity nester species in closed-canopy forest. In addition, the presence of this excavator's cavity tree was better at predicting cavity nester species richness in stands than could other excavators or null models. Sites with a Pileated Woodpecker cavity tree had on average 1.5 more cavity-nesting species than polygons with cavity trees of the most abundant smaller woodpecker species, the Yellow-bellied Sapsucker.

The white-backed woodpecker (*Dendrocopos leucotos*) is considered an umbrella species in Fennoscandia (Martikainen et al. 1998, Virkkala 2006, Roberge et al. 2008, Bell 2015). Its conservation was associated with the conservation of saproxylic

beetles, as these species share the need for deciduous dead wood. Similarly, the Siberian flying squirrel (*Pteromys volans*) was identified as an umbrella species for polypore species (Hurme et al. 2008). It is probable that the Pileated woodpecker plays a comparable role for similar species in North American boreal forests. Our results suggest that the habitat strongly selected by this excavator, old mixedwoods with trembling aspen are very important habitats for most cavity nesters, which represents a considerable proportion of biodiversity in the boreal forest (chapters 1 et 2). Given that old boreal mixedwoods are also considered to be habitats of special concern for the conservation of many other species than cavity users, the Pileated Woodpecker could, by extension, be an umbrella species for these other organisms (birds - Schieck and Song 2006 and Drever et al. 2008; cavity users - Martin et al. 2004 and Cooke and Hannon 2011; mammals - Crête and Courtois 1997, Potvin et al. 2000 and Cheveau et al. 2013; insects - Komonen 2003). However, more research is needed to validate this in the field. In the meantime, old boreal mixedwoods stands should be considered key habitats, a term derived from keystone species due to their importance for the conservation of overall biodiversity in the boreal forest (Hansson 2001).

Conservation efforts for cavity nesters in boreal forest should be aimed at old-growth mixedwood forests with old and large decaying and dead trembling aspen. The use of the Pileated Woodpecker as an umbrella species could be very useful since these forests are becoming rarer in the southern portion of the boreal forest since management has drastically changed the proportion of old forests in the landscape (Bergeron et al. 2004, Cyr et al. 2009) whereas, in the northern portion of boreal forest, mixedwoods are scattered and rare (Gauthier et al. 2000). We need adequate indicator and umbrella species for evaluating and monitoring how managed forest landscapes keep key habitats (old forest stands) and key structural elements (decaying and deadwood) that are not only critical for the maintenance of the cavity-nesting

community but which will ensure the maintenance of biodiversity as a whole (Drapeau et al. 2009b, Drapeau et al. 2009c).

3.6.3 Scope and limitations of using the Pileated Woodpecker as an umbrella species

The Pileated Woodpecker can be considered an umbrella species for the community of cavity nesters in closed–canopy mixedwoods throughout the boreal forest. Hence, while mixedwood stands become marginal habitats at northern latitudes, they nevertheless harbor most of the cavity-nesting community that characterizes southern boreal mixedwood stands, including the Pileated Woodpecker (chapters 1 and 2). The status of umbrella species for the Pileated Woodpecker thus holds in the conifer-dominated matrix of the northern region of the boreal. However, as coniferous stands dominate the forest matrix, the Black-backed Woodpecker and the American Three-toed Woodpecker become important cavity excavators. In the Canadian eastern boreal forest, these excavators are not associated with closed-canopy mixedwood forests but rather with open and perturbed conifer-dominated forested habitats, e.g. forests flooded by the American beaver, edge of forest cuts, burns (chap 2, (Nappi et al. 2003, Nappi and Drapeau 2009, Nappi et al. 2010) or in old productive conifer stands (Tremblay et al. 2009 and chapter 2). In the conifer-dominated boreal forest we thus reiterate Lambeck's (1997) point to use a suite of focal species instead of single indicator species which can better reflect specific habitat requirements of both mixedwood and the coniferous component of this forest region. Hence, we propose that the Pileated Woodpecker be combined with a suite of other umbrella or focal species that would represent other specific needs (Lambeck 1997, Roberge and Angelstam 2004, Drapeau et al. 2009b, Cheveau 2015).

Our empirical study clearly shows that it is likely that a conservation strategy aimed at the habitat of the Pileated Woodpecker will ensure the conservation of rich and complex cavity-nesting networks in mixedwood stands of the boreal forest.

Complementary indicators should, however, be developed for coniferous stands which represent the dominant large-scale forest cover types in the boreal forest.

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3.9 Tables

Table 3.1. List of habitat variables at the stand and landscape scale taken from digital cover maps and used for habitat selection by cavity nesters.

Variable	Description	Range
Stand variables	Polygons from digital cover maps	
Area	Polygon size (ha)	0.05-9.4
Conif	Proportion of coniferous cover	0-75
Aspen	Proportion of trembling aspen cover	0-75
Height	Stand height (m)	0-25
Dens	Overstory density (%)	0-100
Age	Stand age	0-120
Landscape variables	Measured in a 700m radius (154 ha)	
Aspen700	Proportion of stands with trembling aspen (>70 years)	0-61
Age90_700	Proportion of old stands (>90 years)	0-77
DivTree700	Diversity of tree species	0-2.08
Conif700	Proportion of coniferous stands	0-90
For<30_700	Proportion of young forests and forest cuts (<30 years)	2-86
DM700	Proportion of mixedwood and deciduous stands	0-88

Table 3.2. List of candidate models and hypotheses for habitat selection at the stand and landscape scale. In order to take into account the hierarchical sampling design, *Plot* is added as a random variable and *Area* is added as an offset in every model.

Models tested	Hypotheses
Stand scale (LH)	
Conif	H1: Stands with a low proportion of coniferous cover will be selected, since they contain more trees adequate for cavity excavation and for foraging.
Aspen	H2: Stands with trembling aspen will be selected since most cavity trees found in the area are trembling aspen.
Height	H3: Tall stands will be selected since the height of a stand is strongly correlated with the diameter of trees and most cavity trees used in the area have a dbh > 30 cm.
Dens	H4: Species associated to open forested habitats will select habitats with low density.
Age	H5: Old forest stands will have a greater probability of being selected since they often contain large senescent and dead trees.
Conif + Dens	H1 + H4
Conif + Age	H1 + H5
Conif x Age	H6: Cavity nesters will select old forest stands but will prefer old mixedwood and deciduous stands.
Aspen + Dens	H2 + H4
Aspen + Age	H2 + H5
Aspen x Age	H8: Cavity nesters will select old stands but will prefer those with trembling aspen.
Height + Dens	H3 + H4
Landscape scale (154 ha)	
Aspen700 + LH	H9: Stands will have a higher probability of being selected if surrounded by mature to old forests with trembling aspen.
Age90_700 + LH	H10: Stands will have a higher probability of being selected if surrounded by old forests (> 90 years).
DivTree700 + LH	H11: Stands will have a higher probability of being selected if surrounded by a high tree species diversity in neighboring stands.
Conif700 + LH	H12: Stands will have a lower probability of being selected if surrounded by coniferous forests.
For<30_700 + LH	H13: Stands will have a lower probability of being selected if surrounded by young forests and forest cuts. However, this will be selected by species associated to open habitats.
DM700 + LH	H14: Stands will have a higher probability of being selected if surrounded by deciduous and mixedwood stands.

HL = local habitat

Table 3.3. Number of cavity trees, number of polygons with cavity trees, proportions of cavity tree that are in trembling aspen and specificity to polygons with a forest height of > 10 m for all cavity nester species found. Cavity trees and nests were found during two cavity search surveys done in 106 plots 2008-2015 in northwestern Quebec, Canada. Species were considered beneficiary species if at least one nest was found in closed-canopy forests.

	Nest tree scale		Polygon scale		
Cavity nester species	Number of cavity trees	Proportion of cavity trees that are trembling Aspen	Number of polygons with cavity trees	Specificity to polygons >10 m	Expected beneficiary species
Black-capped Chickadee	8	50 %	8	63 %	Yes
Boreal Chickadee	4	13 %	4	75 %	Yes
Red-breasted Nuthatch	44	77 %	32	97 %	Yes
Downy Woodpecker	43	96 %	35	97 %	Yes
Yellow-bellied Sapsucker	151	99 %	89	93 %	Yes
American Three-toed Woodpecker	1	0 %	1	0%	
Black-backed Woodpecker	0	0 %	0	0%	
Hairy Woodpecker	20	87 %	14	93 %	Yes
Northern Flicker	58	66 %	47	55 %	Yes
Pileated Woodpecker[b]	64	98 %	38	95 %	Yes
Red squirrel	9	100 %	8	75 %	Yes
Northern flying squirrel	26	96 %	25	88 %	Yes
Hooded Merganser	9	100 %	9	89 %	Yes
Common Goldeneye	13	92 %	13	92 %	Yes
Northern Saw-whet Owl	3	100 %	3	100 %	Yes
American Kestrel	7	29 %	6	33 %	Yes
Tree Swallow	5	0 %	5	0 %	
Common Grackle	8	43 %	8	0 %	
Bufflehead	2	50 %	2	0 %	
Total	425	84 %	149[a]	79 %	

[a] Total number of polygons is not the sum of the columns because some polygons have nests or cavity trees from multiple species

[b] Pileated Woodpecker cavity trees were used in the analysis whether or not the cavities contained nests

Table 3.4. Model selection results at stand and landscape scales for habitat selection by cavity nesters. Grouped cavity users represent species richness of 10 species for which < 20 polygons with cavity trees were found. The offset *Area* and the random effects *Plots* are included in each model. We present all the models with a $\Delta AIC_c < 2$. Model fit was evaluated with a pseudo-R^2 (R^2). The fit of bootstrapped predictions to observations for single species HSM was evaluated with Cohen's Kappa statistic (κ). In the case of multi-species models we evaluated this fit with spearman correlation (Spear.Cor) and with the beta of a linear regression (±SE).

Species	Scale	Models	K	AIC_c	ΔAIC_c	Diagnostics of models
Downy Woodpecker	Stand	Aspen	3	174.3	0	κ= 0.39, R^2= 0.14
	Landscape + stand	DM700 + Aspen	4	160.2	0	κ= 0.39, R^2= 0.24
Yellow-bellied Sapsucker	Stand	Aspen x Age	5	254.7	0	κ= 0.55, R^2= 0.26
	Landscape + stand	Conif700 + Aspen x Age	6	245,5	0	κ= 0.54, R^2= 0.31
		DivTree700 + Aspen x Age	6	245,8	0.30	κ= 0.56, R^2= 0.31
Northern Flicker	Stand	Aspen	3	174.4	0	κ= 0.22, R^2= 0.06
		Aspen x Age	5	175.2	0.90	κ= 0.25, R^2= 0.08
	Landscape + stand	For<30_700 + Aspen	4	160.8	0	κ= 0.29, R^2= 0.17
		For<30_700 + Aspen x Age	6	161.7	1.16	κ = 0.32, R^2= 0.19
Pileated Woodpecker	Stand	Aspen x Age	5	147.7	0	κ= 0.54, R^2= 0.32
	Landscape + stand	DivTree700 + Aspen x Age	6	144.1	0	κ= 0.53, R^2= 0.36
Grouped cavity users	Stand	Aspen	3	195.8	0	Spear.Cor= 0.65 β= 1.56 (±0.06) R^2= 0.24
		Aspen x Age	5	196.4	0.52	Spear.Cor= 0.67 β= 1.58 (±0.06) R^2= 0.26
	Landscape + stand	DivTree700 + Aspen	4	187.6	0	Spear.Cor= 0.69 β= 1.32 (±0.06) R^2= 0.29
		Age90_700 + Aspen x Age	6	189.2	1.62	Spear.Cor= 0.70 β= 1.50 (±0.06) R^2= 0.31
		DivTree700 + Aspen x Age	6	190.0	1.91	Spear.Cor= 0.59 β= 1.37 (±0.06) R^2= 0.29

Table 3.5. Estimated parameter values of best HSM models for the stand and landscape scale ($\Delta AIC_c < 2$). Grouped cavity users represent species richness of 10 species for which > 20 polygons with cavity trees were found. Parameters and 95 % confidence intervals were calculated using a bootstrapping procedure with 1000 permutations. Values in bold have 95 % confidence intervals that do not include the zero.

Response Variable	Model number[a]	Explanatory variables	Estimated parameter value (CI 95 %)
Pileated Woodpecker	1	Aspen	**1.69 (1.12, 2.69)**
		Age	0.35 (-0.45, 1.06)
		Aspen * Age	**1.21 (0.47, 2.29)**
		DivTree700	**0.91 (0.14, 1.83)**
Yellow-bellied Sapsucker	1	Aspen	**0.94 (0.64, 1.31)**
		Age	-0.24 (-0.59, 0.09)
		Aspen * Age	**0.64 (0.27, 1.06)**
		DivTree700	**0.52 (0.17, 0.97)**
	2	Aspen	**0.88 (0.56, 1.23)**
		Age	-0.12 (-0.46, 0.20)
		Aspen * Age	**0.56 (0.18, 1.04)**
		Conif700	**-0.80 (-1.40, -0.34)**
Downy Woodpecker	1	Aspen	**0.90 (0.48, 1.43)**
		DM700	**1.39 (0.70, 2.65)**
Northern Flicker	1	Aspen	**0.71 (0.30, 1.17)**
		For<30_700	**0.89 (0.48, 1.44)**
	2	Aspen	**0.87 0.59 1.15**
		Age	-0.12 -0.42 0.18
		Aspen * Age	0.27 -0.03 0.62
		For<30_700	**0.27 0.02 0.51**
Grouped cavity users	1	Aspen	**0.92 (0.68, 1.21)**
		DivTree700	**0.58 (0.22, 0.94)**
	2	Aspen	**0.94 (0.68, 1.23)**
		Age	0.13 (-0.21, 0.48)
		Aspen * Age	**0.43 (0.08, 0.80)**
		Age90_700	**-0.43 (-0.69, -0.16)**
	3	Aspen	**0.95 0.67 1.26**
		Age	-0.04 (-0.31, 0.24)

	Aspen * Age	0.26 (-0.08, 0.59)
	DivTree700	**0.55 (0.20, 0.92)**

[a] Relevant when there are multiple closely competing models (Delta-AIC_c<2).

Table 3.6. Estimated parameter values of the HSM of the Downy Woodpecker, the Yellow-bellied Sapsucker and the Pileated Woodpecker on the species richness for polygons. GLMM were done on three levels of the response variable species richness: all expected beneficiary species, cavity excavators and secondary cavity nesters. A pseudo-R^2 based on the likelihood-ratio test is computed for each model by comparing the model to a null model containing the offset *Area* and the random effect *Plot*. All estimated values differed significantly from zero.

Response Variable	Excavator species	HSM (CI 95 %)	Pseudo- R^2
All expected beneficiary species	Downy Woodpecker	**0.62 (0.51, 0.74)**	0.17
	Yellow-bellied Sapsucker	**1.07 (0.87, 1.32)**	0.32
	Pileated Woodpecker	**0.57 (0.49, 0.67)**	0.32
Cavity excavator	Downy Woodpecker	**0.57 (0.45, 0.69)**	0.17
	Yellow-bellied Sapsucker	**0.98 (0.77, 1.23)**	0.27
	Pileated Woodpecker	**0.53 (0.45, 0.63)**	0.26
Secondary cavity nesters	Downy Woodpecker	**0.71 (0.49, 1.01)**	0.15
	Yellow-bellied Sapsucker	**1.29 (0.94, 1.87)**	0.28
	Pileated Woodpecker	**0.77 (0.59, 1.02)**	0.33

3.10 Figures

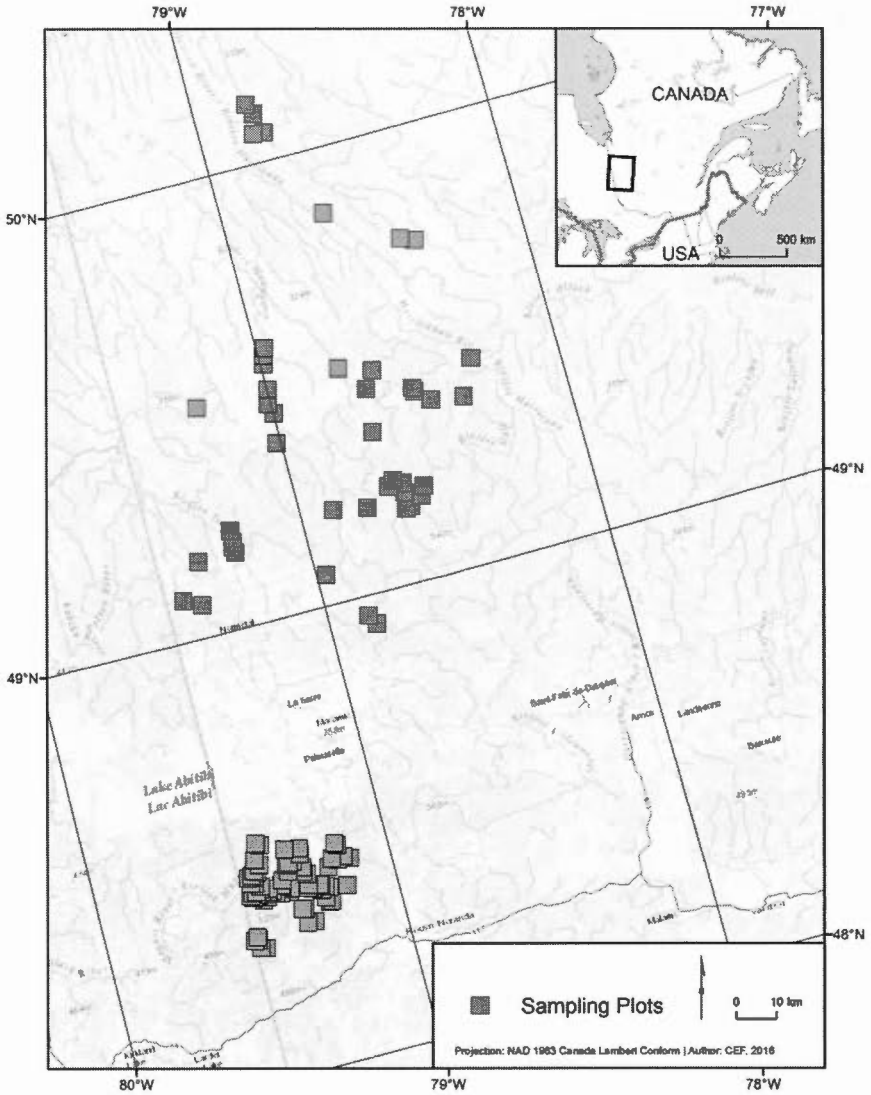
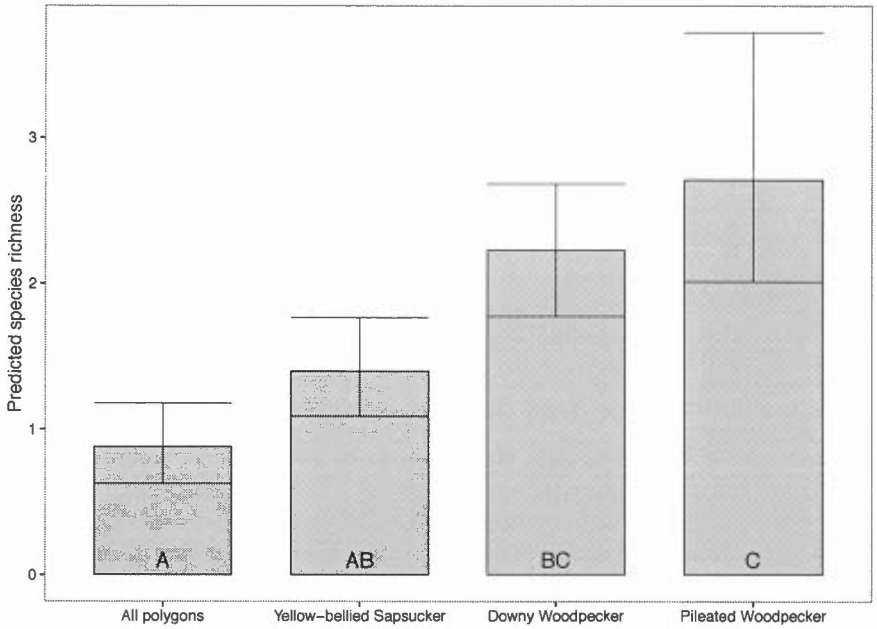
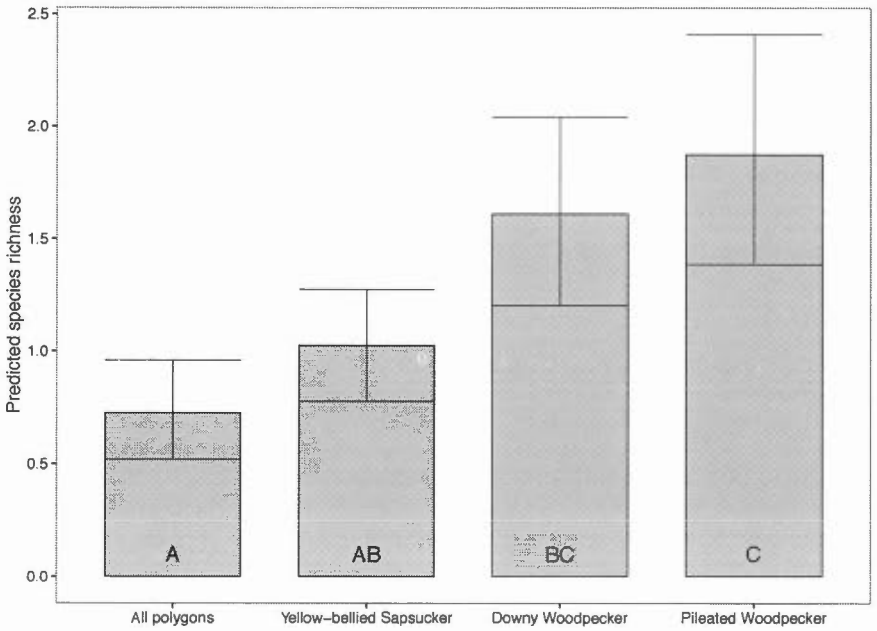


Figure 3.1. Location of study sites in northwestern Québec, Canada.

a) All expected beneficiary species



b) Cavity excavators species richness



c) Secondary cavity nester species richness

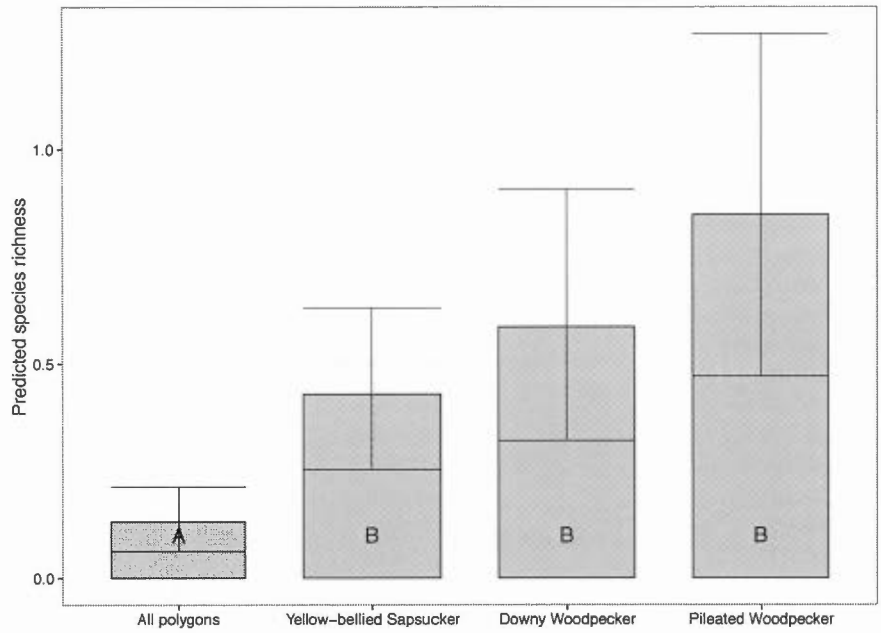
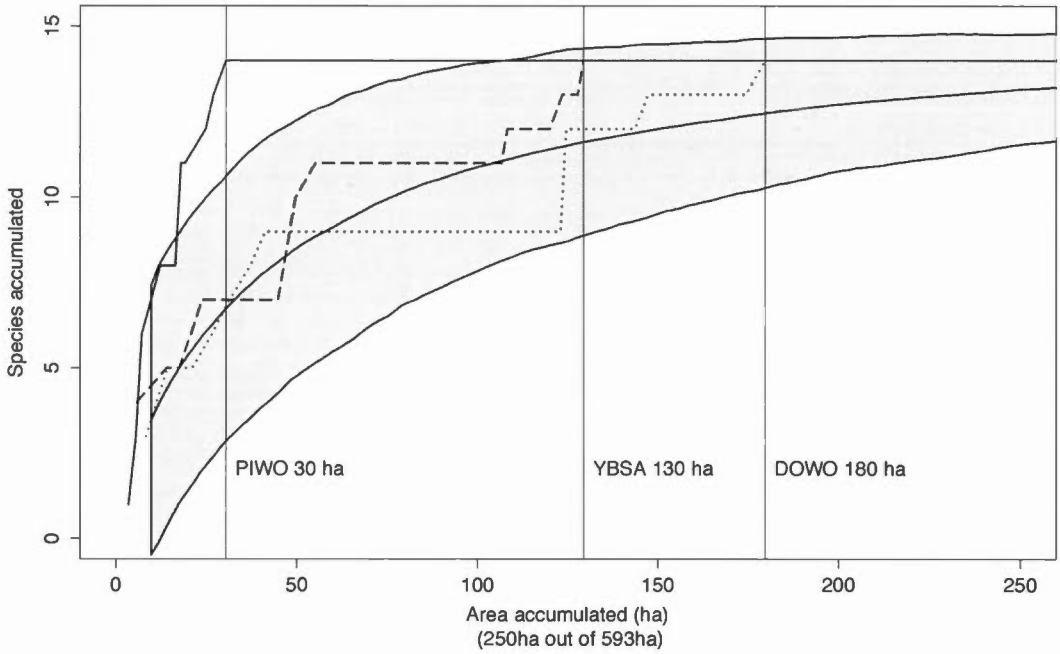
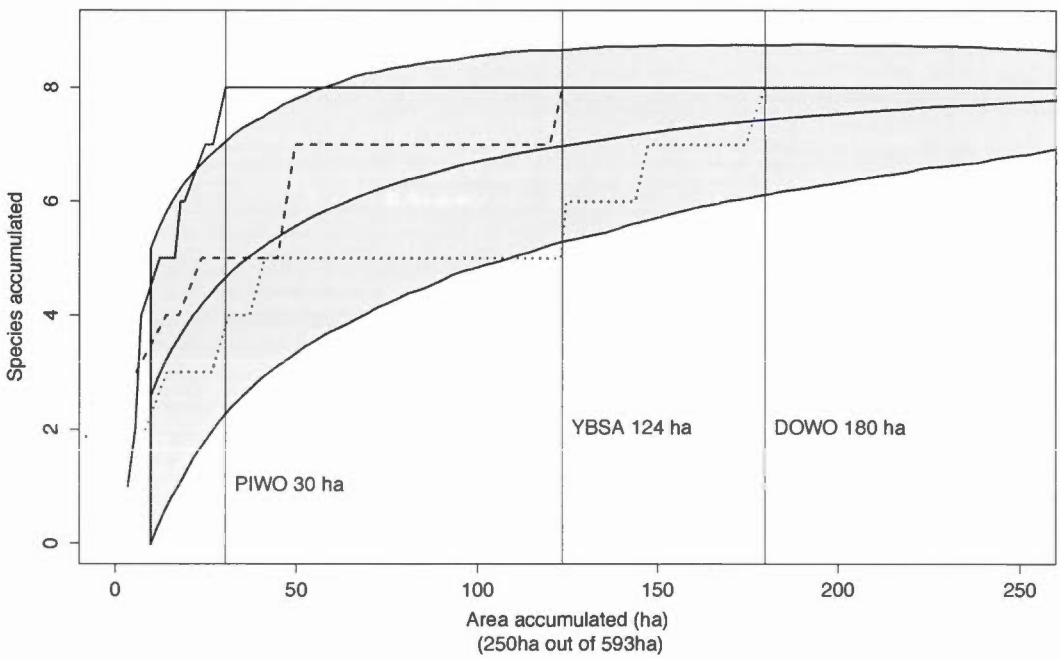


Figure 3.2. Predictions of the average species richness for polygons where there was at least one cavity tree of the focal excavator. GLMMs were done on three levels of the response variable species richness: a) all expected beneficiary species, b) cavity excavators and c) secondary cavity nesters. Letters represent statistically significant differences where the confidence intervals do not overlap. The predictions and 95 % confidence intervals were calculated using a bootstrapping procedure with 1000 permutations for a polygon size of 3 ha.

a) All expected beneficiary species



b) Cavity excavators species richness



c) Secondary cavity nester species richness

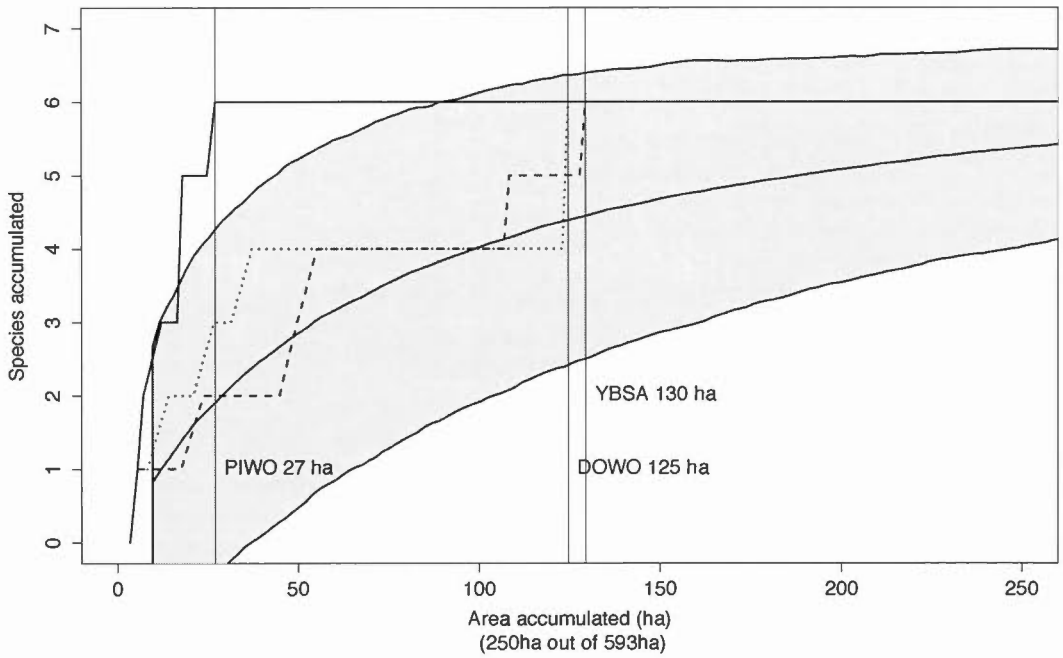


Figure 3.3. Species accumulation curves based on random resampling of all polygons (gray polygon) and collectors' curves ordered by the HSMs of the Downy Woodpecker (smaller dashed lines), the Yellow-bellied Sapsucker (larger dashed lines) and the Pileated Woodpecker (full lines). Vertical lines indicate where the maximum number of species is attained for the collectors' curves. The species accumulation curves are plotted against the polygon area size accumulation and were done on three levels of the response variable species richness: All expected beneficiary species, cavity excavators and secondary cavity nesters.

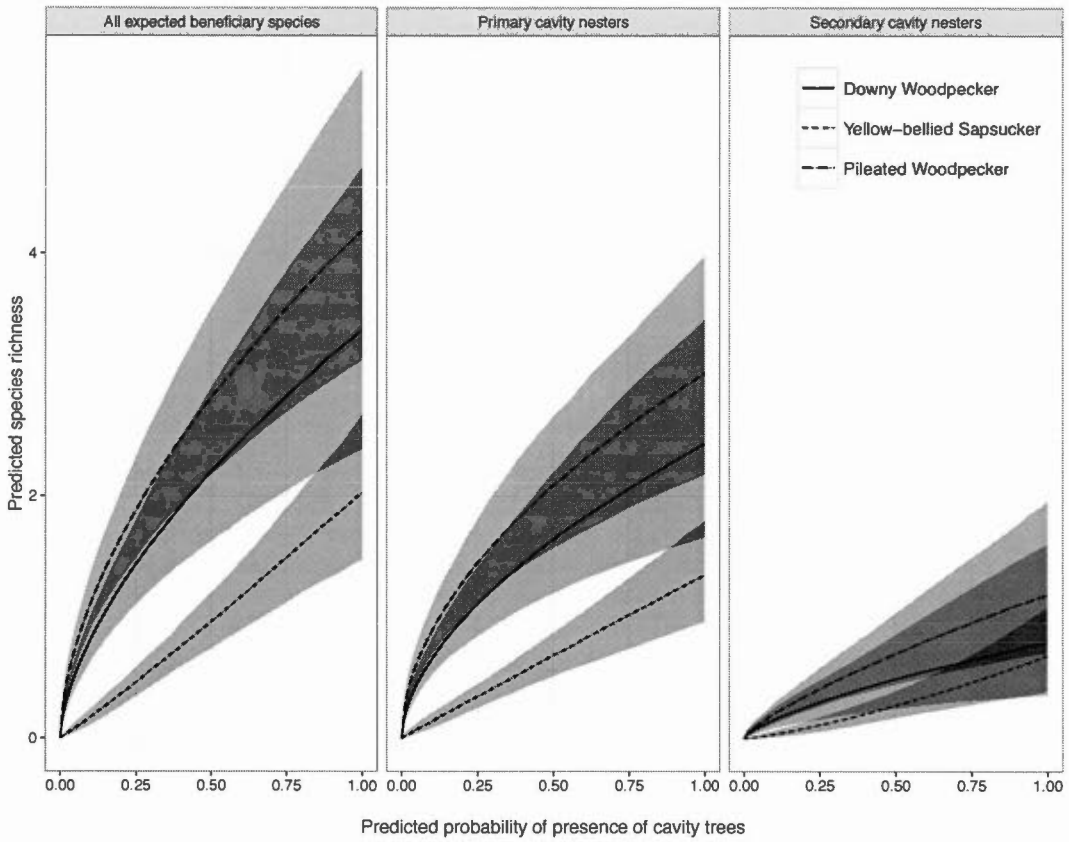


Figure 3.4. Predicted species richness as a function of the predicted probability of presence calculated with HSMs of the Downy Woodpecker (full lines), the Yellow-bellied Sapsucker (smaller dashed lines) and the Pileated Woodpecker (larger dashed lines). GLMMs were computed for three levels of the response variable species richness: a) All expected beneficiary species, b) cavity excavators and c) secondary cavity nesters. The predictions and 95 % confidence intervals (gray bands) were calculated using a bootstrapping procedure with 1000 permutations.

3.11 Appendix A

Table 3A. Estimated parameter values of the size of polygons on species richness for polygons where there was at least one cavity tree of the focal excavator. GLMMs were done on three levels of the response variable species richness: All expected beneficiary species, cavity excavators and secondary cavity nesters. The parameters and 95 % confidence intervals were calculated using a bootstrapping procedure with 1000 permutations. Values in bold are significant as their 95 % confidence intervals do not include zero.

Response Variable	Excavator species	Area (CI 95 %)
All expected beneficiary species	Downy Woodpecker	**0.22 (0.04, 0.56)**
	Yellow-bellied Sapsucker	**0.36 (0.15, 0.60)**
	Pileated Woodpecker	**0.37 (0.16, 0.72)**
	Null model	**1.08 (0.97, 1.22)**
Cavity excavator	Downy Woodpecker	0.19 (-0.05, 0.50)
	Yellow-bellied Sapsucker	**0.40 (0.16, 0.65)**
	Pileated Woodpecker	**0.42 (0.12, 0.84)**
	Null model	**0.99 (0.85, 1.12)**
Secondary cavity nesters	Downy Woodpecker	0.38 (-0.10, 1.11)
	Yellow-bellied Sapsucker	0.08 (-0.21, 0.58)
	Pileated Woodpecker	0.37 (-0.11, 0.98)
	Null model	**1.01 (0.66, 1.35)**

CONCLUSION GÉNÉRALE

Cette thèse démontre que l'avifaune associée au bois mort est grandement dépendante des vieilles forêts boréales. Ces forêts sont distribuées sur l'ensemble du territoire et assurent un apport constant d'arbres morts et sénescents. Toutefois, le long de l'important gradient latitudinal de transition d'un couvert forestier mixte à résineux, on observe une réduction considérable de la disponibilité d'arbres morts et sénescents de qualité pour la nidification et l'alimentation de ce groupe fonctionnel d'espèces (Gauthier et al. 2000, Drapeau et al. 2009). Nous montrons que cette réduction des arbres à cavités en pessière à mousses organise les réseaux d'utilisateurs de cavités autour des peuplements mixtes isolés ainsi que dans les forêts inondées par les castors tandis que les forêts âgées résineuses supportent une plus faible richesse en espèces associées au bois mort ainsi que des réseaux d'utilisateurs de cavités moins diversifiés et moins complexes. Des habitats ainsi que des espèces clés de voûte sont identifiés et cette thèse approfondit notre compréhension de leurs rôles respectifs dans la structure des communautés d'oiseaux cavicoles de l'écosystème boréal tant en sapinière à bouleau blanc qu'en pessière à mousses. Une espèce en particulier, le Grand Pic joue le rôle d'espèce parapluie alors que sa sélection fine des habitats de reproduction recoupe fortement les exigences de l'habitat de reproduction de la majorité des autres espèces cavicoles. Nous pouvons résumer l'apport des connaissances acquises dans cette thèse sous trois dimensions : la diversité spécifique, la diversité fonctionnelle et les espèces indicatrices de l'écosystème boréal.

Diversité spécifique des oiseaux associés au bois mort en pessière à mousses

Les deux premiers chapitres apportent de nouvelles connaissances concernant l'importance de l'âge, de la productivité et de la composition des forêts pour l'occurrence, l'alimentation (chapitre 1) et la nidification (chapitre 2) de l'avifaune associée au bois mort en pessière à mousses.

Les forêts âgées de conifères en pessière à mousses non entourbées étaient plus utilisées que les forêts matures par le groupe d'espèces d'oiseaux associées au bois mort. Toutefois, ce ne sont pas toutes les forêts âgées qui offraient des conditions adéquates pour ce groupe focal d'espèces. L'entourbement des forêts résineuses a eu un effet négatif important sur l'occupation et l'utilisation de l'habitat par l'avifaune associée au bois mort. Ainsi, après les forêts matures (avec peu de bois sénescent et mort) les forêts entourbées (> 160 ans) ont vu leur richesse spécifique ainsi que l'activité d'alimentation des pics (traces fraîches d'alimentation) diminuer par rapport aux forêts âgées non entourbées. L'avifaune associée au bois mort a donc montré une distribution modale en réponse au vieillissement de la forêt et à la baisse de productivité forestière. Les résultats du chapitre 1 montrent donc clairement que la richesse spécifique et l'abondance de traces d'alimentation de pics sont liées à une abondance accrue de bois mort et une plus grande diversité structurale dans ces vieilles forêts.

Nos résultats montrent clairement que les vieilles forêts mixtes avec peupliers faux-trembles sont des habitats clés et sont fortement sélectionnés par l'avifaune associée au bois mort en pessière à mousses. Ainsi, malgré leur faible représentation dans le paysage (4 %) et le fait qu'ils étaient en général isolés par de grandes étendues de forêts résineuses ou de tourbières, l'abondance des oiseaux associés au bois sénescent et mort dans les forêts mixtes de la pessière à mousses a montré une forte ressemblance à celles de la sapinière à bouleau blanc. Dans ces habitats, nous avons

trouvé la plus grande richesse spécifique, les plus grandes abondances de traces d'alimentation de pics et les réseaux d'utilisateurs de cavités les plus riches.

Il y avait un fort contraste entre les forêts âgées mixtes et les forêts âgées résineuses qui étaient beaucoup moins prisées par la faune cavicole, et ce malgré un effort d'échantillonnage considérable (chapitre 2), très peu de nids et d'arbres à cavités ont été trouvés en forêts résineuses. Malgré la faible abondance de nids trouvés dans les forêts âgées résineuses non entourbées (chapitre 2), ces dernières étaient fortement utilisées par le Pic à dos noir et le Pic à dos rayé pour leur alimentation (chapitre 1).

Diversité fonctionnelle de l'avifaune associée au bois mort

Les réseaux d'utilisateurs de cavités de l'Amérique du Nord sont composés d'une faible proportion d'espèces ayant beaucoup de liens et de peu de redondance dans leurs rôles fonctionnels (Cockle et al. 2012, Simard et al. 2013). Ceci suggère une faible robustesse à la perte des espèces qui soutiennent beaucoup de liens (Messier et al. 2013). Le long du gradient latitudinal, les changements importants dans la disponibilité des arbres adéquats à l'excavation de cavités, tels qu'observés au chapitre 1, ont le potentiel de changer la structure des réseaux au niveau des arbres à cavités et des excavateurs de cavités. Avec une perspective régionale, le chapitre 2 apporte de nouvelles connaissances portant sur la robustesse, le changement et la persistance des réseaux d'utilisateurs de cavités soumis à la perte de ressources en bois mort et sénescent.

Bien que les réseaux d'utilisateurs de cavités se prêtent bien au cadre conceptuel et théorique de l'analyse des réseaux complexes en écologie (Sole et Montoya 2001, Dunne et al. 2002, Fath et al. 2007), les réseaux d'utilisateurs de cavités trouvés dans la littérature restent (Martin et Eadie 1999, Blanc et Walters 2007, Simard et al. 2013), à ce jour, des structures descriptives utilisées principalement pour représenter

les interactions entre les espèces (Blanc et Walters 2007) (mais voir Cadieux 2011 et Cockle et al. 2012). Le chapitre 2 est l'une des premières études à analyser à une échelle régionale les changements de structure des réseaux d'utilisateurs de cavités en fonction de la variation du couvert forestier et en corollaire, de la disponibilité des arbres à cavités dans différents paysages forestiers. Grâce à des données récoltées à long terme (2003-2015) et sur un vaste territoire chevauchant deux régions bioclimatiques (12 000 km^2), cette étude aborde la question de la robustesse de ces réseaux soumis à d'importants changements écologiques. À l'aide d'une analyse de retrait ciblé d'espèces, nous montrons que les réseaux d'utilisateurs de cavités dans les peuplements fermés de la forêt boréale sont peu robustes à la perte d'espèces clés. La simulation de la perte du peuplier faux-tremble cause > 70 % d'extinctions secondaires dans ces forêts, et ce même dans la région de la pessière à mousses. Malgré leur faible représentation régionale, les forêts mixtes de peupliers faux-trembles conservent un rôle de premier plan dans la structure des réseaux d'utilisateurs de cavités en pessière à mousses. Nos résultats indiquent toutefois que la répartition nordique de certaines espèces de pics est fortement liée à cette essence.

Bien que les forêts inondées par le castor d'Amérique sont généralement considérées comme des environnements importants pour les écosystèmes riverains et la diversité biologique (Naiman et al. 1986, Macdonald et al. 1995, Stockland et Siitonen 2012, Smith et Mather 2013), le chapitre 2 compte parmi les premières études à quantifier l'importance de cet habitat dans la création d'arbres de nidification pour la faune cavicole. Nos résultats montrent que les forêts inondées par l'activité du castor contribuent de manière importante aux réseaux d'utilisateurs de cavités sur l'ensemble de la forêt boréale. Cependant, ces habitats, de pair avec les forêts mixtes, sont encore plus importants en pessière à mousses vu la faible disponibilité d'habitats adéquats pour la nidification. Ces réseaux étaient riches et robustes à la perte du peuplier faux-tremble, étant moins dépendants à cette essence comparativement aux forêts fermées. L'ennoiement des arbres par le castor crée des arbres adéquats à

l'excavation de cavités et à la nidification d'espèces cavicoles associées aux forêts à canopées ouvertes sans propension marquée pour l'essence.

En incorporant l'analyse des réseaux d'utilisateurs de cavités des forêts perturbées par le castor, nos travaux apportent non seulement une nouvelle perspective au rôle écologique de ces habitats dans le maintien de la diversité fonctionnelle en forêt boréale, mais ils élargissent notre compréhension des réseaux d'utilisateurs de cavités dans l'écosystème boréal et de l'importance des étangs à castors pour la faune cavicole.

Espèces indicatrices de diversité

Tel que vu dans plusieurs autres études, deux excavateurs de cavités de taille moyenne à grande se sont démarqués comme excavateurs clés dans notre étude, le Grand Pic et le Pic flamboyant (Bonar 2000, Aubry et Raley 2002, Martin et al. 2004, Blanc et Walters 2008a, Cooke 2009, Cadieux 2011). Le Grand Pic était l'excavateur dont les cavités étaient les plus réutilisées par les plus grandes espèces cavicoles. Notre étude apporte de nouvelles connaissances quant à la persistance de ce rôle dans les peuplements mixtes isolés dans le domaine bioclimatique de la pessière à mousses. Le Pic flamboyant était l'excavateur ayant le plus de cavités réutilisées en forêts ouvertes, et ce notamment pour les forêts ennoyées par le castor. La contribution de ces deux ingénieurs écologiques affecte la structure de réseaux complexes d'utilisateurs de cavités dans la région de la pessière à mousses.

Bien que plusieurs chercheurs et aménagistes forestiers aient proposé ou encore utilisent le Grand Pic comme espèce parapluie (McClelland et al. 1979, Bull et al. 1992, Blanchette 1996, McLaren et al. 1998, McClelland et McClelland 1999, Savignac et al. 2000, Aubry et Raley 2003, Lemaître et Villard 2005, Cheveau 2015), il n'existe à notre connaissance aucune étude qui n'aient vérifié de façon formelle

l'hypothèse que les exigences d'habitat de reproduction Grand Pic puissent recouper celles d'autres espèces, notamment du groupe fonctionnel des utilisateurs d'arbres à cavités. Les chapitres 2 et 3 permettent de conclure que le Grand Pic joue le double rôle d'espèce clé de voûte et d'espèce parapluie pour la faune cavicole associée aux forêts mixtes tant en sapinière à bouleau blanc qu'en pessière à mousses de la forêt boréale de l'est du Canada. Une série de tests effectués au chapitre 3 permettent de confirmer le statut d'espèce parapluie de cet excavateur pour la faune cavicole. Le Grand Pic sélectionne fortement les peuplements qui sont également convoités par la majorité de la faune cavicole, les vieilles forêts mixtes composées de peupliers faux-trembles sénescents de fort diamètre. Cette sélection vient corroborer le rôle clé joué par les forêts mixtes âgées (chapitres 1 et 2) pour les réseaux écologiques d'utilisateurs de cavités en forêt boréale. Cependant, le chapitre 3 précise que les paramètres d'habitat de nidification du Grand Pic sont non seulement aptes à convenir aux espèces utilisatrices de ses cavités (utilisateurs secondaires de grande taille), mais à tout le réseau d'espèces cavicoles (y compris les excavateurs et utilisateurs de petites et moyennes cavités). L'habitat du Grand Pic en forêt boréale offre donc une option clé pour la planification de la conservation des réseaux d'utilisateurs de cavités, qui représentent un contingent important de la diversité spécifique et fonctionnelle des écosystèmes en forêt boréale.

Implications en aménagement forestier

La sénescence et la mort des arbres sont critiques pour de nombreuses espèces en forêt boréale. Nous devons pratiquer une gestion de nos forêts qui ne cause pas une trop forte diminution de la disponibilité de ces attributs dans nos paysages forestiers (Jonsson et al. 2005, Stockland et Siitonen 2012). Une des conclusions importantes de cette thèse renvoie à l'importance des vieilles forêts productives comme habitats clés pour le maintien de la diversité spécifique et fonctionnelle de la faune vertébrée associée au bois mort et sénescent. Cette thèse propose de plus que certaines espèces,

comme le Grand Pic (chapitre 3), puissent être des indicateurs dans la planification de la rétention d'habitats de qualité pour l'ensemble du réseau cavicole dans les territoires aménagés. De plus, cette espèce pourrait aussi servir d'outil d'évaluation de l'efficacité de l'aménagement durable des forêts à maintenir la diversité fonctionnelle des utilisateurs de bois mort en forêt aménagée (Drapeau et al. 2008).

Les vieilles forêts mixtes devraient bénéficier d'une attention particulière de protection vu leur grande richesse et leur faible représentation dans le paysage, surtout en région de pessière à mousses.

Contrairement à d'autres écosystèmes forestiers, les vieilles forêts résineuses en pessière à mousses ne contribuent pas toutes de la même façon aux réseaux d'utilisateurs de cavités. Leur entourbement progressif diminue grandement leur capacité à offrir des conditions adéquates de bois sénescent et mort pour les réseaux d'utilisateurs de cavités (chapitres 1 et 2). Plusieurs espèces cavicoles et corticoles sont donc influencées par cette diminution marquée dans la disponibilité d'arbres morts ou sénescents de grande taille. Planifier la conservation du réseau des utilisateurs de cavités dans les forêts de conifères exige donc de concentrer les efforts sur les forêts âgées productives, qui sont également convoitées par l'industrie. On ne peut penser assurer le maintien de la faune cavicole associée aux forêts résineuses de la pessière à mousses en portant nos stratégies de rétention de forêts âgées sur les vieilles forêts entourbées. Celles-ci ne peuvent donc être considérées comme de bons habitats pour la faune associée au bois mort.

Enfin, les forêts inondées constituent des habitats clés pour une portion importante de la communauté d'espèces cavicoles en forêt boréale. La conservation de ces habitats constitue une stratégie peu coûteuse considérant que ces habitats ne sont généralement pas considérés comme productifs et potentiellement exploitables sur le plan ligneux.

Perspectives futures de recherche

Cette thèse appuie l'idée que les vieilles forêts mixtes avec peupliers faux-trembles sont critiques pour le maintien de la diversité de la faune associée au bois mort pour l'ensemble de la forêt boréale, et ce indépendamment de la composition régionale de la matrice forestière. Bien que nous ayons documenté l'utilisation de ces forêts pour la reproduction et l'alimentation de la faune cavicole, des études sur la productivité des individus nicheurs sont nécessaires pour comprendre l'effet de cet isolement sur la valeur sélective (fitness) des individus et statuer sur la contribution démographique de ces habitats. En effet, la distance de ces forêts isolées aux grands massifs de forêts mixtes plus au sud pourrait avoir un impact sur le succès d'appariement des individus reproducteurs ou encore sur le succès des jeunes à l'envol si les ressources alimentaires s'avèrent de moins bonne qualité comme il a déjà été vu chez des passereaux dans des forêts fragmentées (Probst et Hayes 1987, Zanette et al. 2000). De plus, les conditions météorologiques moins clémentes à ces latitudes nordiques pourraient également avoir un impact sur la capacité de nourrir les jeunes au nid (Öberg et al. 2015). Il y aurait alors potentiellement des effets négatifs sur le succès de reproduction et la productivité des nicheurs (nombre moyen de jeunes à l'envol).

Le chapitre 2 démontre que les forêts inondées par le castor sont des habitats où l'on trouve des réseaux d'utilisateurs de cavités riches et complexes et qui ont une grande densité de nids d'espèces cavicoles associées aux forêts ouvertes. Par contre, ce sont aussi les habitats qui ont les cavités arboricoles les plus basses. Il serait important de mesurer la productivité des espèces cavicoles dans ces habitats pour évaluer si ces cavités ne sont pas plus vulnérables à la prédation et qu'ils constituent par conséquent des habitats marginaux par rapport aux forêts fermées quant à leur productivité.

Le Grand Pic est clairement identifié comme espèce parapluie pour la faune cavicole en forêt boréale dans le chapitre 3. D'autres études sont nécessaires pour vérifier si cet excavateur de cavités serait aussi une espèce parapluie pour un plus large éventail d'organismes, comme il a été observé pour le Pic à dos blanc (*Dendrocopos leucotos*) dans les forêts boréales Fenno-scandinaves (Roberge et al. 2008). Vu sa forte sélection des vieilles forêts mixtes avec peuplier faux-tremble, il est fort probable que ce rôle s'applique aussi pour plusieurs autres espèces de vertébrés associées au même habitat (Potvin et al. 2000, Jacqmain et al. 2008, Cheveau et al. 2013).

Dans cette thèse, nous avons trouvé très peu de nids de Pic à dos noir et de Pic à dos rayé, et la grande majorité de ces nids étaient situés dans des forêts inondées par le castor. Cependant, en forêt résineuse à canopée fermée nous avons trouvé beaucoup de traces d'alimentation de ces deux pics et ces espèces étaient souvent aperçues. De nouvelles études sont nécessaires pour mieux comprendre l'utilisation des forêts résineuses non brûlées pour la reproduction de ces deux pics (voir Tremblay et al. 2009, 2015). En l'absence de perturbations majeures comme les feux de forêt, il reste à voir si le Pic à dos noir et le Pic à dos rayé n'utiliseraient pas de façon préférentielle les forêts ennoyées par le castor au détriment des forêts fermées âgées.

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